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LINKING SPATIAL PATTERNS TO FOREST ECOLOGICAL PROCESSES BY USING SPATIAL STATISTICAL METHODS

by

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Linking spatial patterns to forest ecological processes by using spatial statistical methods

Chairman: John M. Goodburn

While spatial patterns have long been recognized as important aspects of forest vegetation and site factors, the task of explaining patterns in relation to underlying processes has been more difficult. Advances in spatial statistical analysis are offering ecologists new strategies for examining spatial patterns that have the potential to better link observed patterns to processes. This dissertation project applied multiple methods of spatial statistical analysis to four field studies conducted in Montana (USA) and Chile (South America), including some novel approaches for examining causal factors and extending the utility of plot-based data. In the first study of natural stands of *Nothofagus glauca* in south-central Chile, analysis using Ripley's L-function indicated that the ecological status of *N. glauca* may vary from pioneer to gap strategist depending on site and stand conditions. On harsh sites, *N. glauca* seedlings displayed positive spatial associations with overstory trees, suggesting facilitation. To further examine bivariate associations observed between regeneration and overstory trees I studied ponderosa pine/Douglas-fir forests of western Montana. A new index was developed that quantifies the strength of association between canopy layers. This index considers the ratio between the value ($\hat{L}_{1.2}(t)$) of the bivariate L-function and the corresponding confidence envelope at a specified distance (t). Larger index values indicate greater departures from the hypothesis of no spatial association, prompting further ANOVA comparisons among groups of plots differing in moisture availability. Seedlings of both ponderosa pine and Douglas-fir tend to be positively associated with overstory trees in drier sites, and negatively associated on moister sites. In a third study examining pine plantations in Patagonia, an effort to further discriminate between multiple factors influencing spatial patterns at different scales utilized a semivariogram approach to formulate stand development models for even-aged populations. In the fourth study, data from ponderosa pine restoration treatments in a randomized block design were weighted using a spatial ANOVA model to control for spatial auto-correlation, allowing expansion of the original design to examine age classes separately. This case study indicated that old trees responded positively to release from competition via harvesting, but that spring broadcast burning may reduce both growth and vigor. These various studies emphasize the importance of both spatial pattern description and the utility of statistical strategies for examining potential causal factors.

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Chapter 1

BACKGROUND, BASIC ANALYTICAL TOOLS, AND POTENTIAL OF SPATIAL PATTERN ANALYSIS FOR EXAMINING FOREST STAND DYNAMICS

> "Everything is related with everything else, but near things are more related than distant things" (Tobler, 1970)

> "We must find ways to quantify patterns of variability in space and time, to understand how patterns change with scale, and to understand the causes and consequences of patterns" (Levin, 1992).

1.1 SPATIAL STATISTICS APPLICATIONS TO PLANT ECOLOGY

Plant ecology has a long history of addressing patterns in vegetation at various scales, ranging from large-scale classification of terrestrial formation types in relation to climate down to individual plant responses to variation in microsites. Clements (1916; 1936) in his theory of successional dynamics stressed temporal dynamics but did not emphasize spatial patterning. However, Gleason (1917; 1926) did state that spatially heterogeneous patterns were important and should be interpreted as individualistic responses to spatial gradients in the environment (Gurevitch et al., 2002). A reconsideration of vegetation patterns in space and time and their relationship with underlying processes was presented by Watt (1947). The primary contribution of Watt is the view of the plant community as a mosaic of patches at different stages in a similar cycle of events, driven by the same processes. It follows that the spatial pattern of this mosaic can be used to generate hypotheses about the underlying processes and/or suggest the mechanisms that have given rise to it (MacArthur, 1972; Dale, 1999). The fundamental point of this conceptualization is that direct relationships can be identified between observed spatial patterns of vegetation and the processes occurring in forest ecosystems, such as seed dispersal, growth, competition, or senescence (Watt, 1947).

1.1.1 Recognizing the importance of pattern and process in plant communities

Both physical and biological variables in nature have been found to display spatial patterns (Legendre, 1993; Dale, 1999; Legendre et al., 2002). We can view natural vegetation as formed by mosaics of patches of different kinds. The size and spacing of these patches are important characteristics of any plant community (Burton and Bazzaz, 1995). Indeed, one of the few generalizations we can make about vegetation is that it is spatially heterogeneous (Dale, 1999). Depending on scale, plant species exhibit different spatial patterns (Greig-Smith, 1979; Legendre and Legendre, 1998). The study of such spatial patterns can be used as a means of inferring simple explanations of complex interspecific processes (MacArthur, 1972). Thus, we expect that ecological processes might give rise to spatially recognizable structures. With the setting of proper a priori hypotheses linking process and pattern, we can potentially infer the processes from the analysis of detected patterns (Watt, 1947; Greig-Smith, 1979; Underwood et al., 2000; Kikvidze et al., 2005; Stoll and Bergius, 2005). In this framework, spatial patterns can be used as a surrogate for underlying processes. However, the opposite is also true. The detection of spatial structures has also been used to enhance the understanding of how patterns of environmental heterogeneity influence ecological processes (Legendre and Fortin, 1989; Turner, 1989; O'Neill et al., 1991; Turner et al., 2001).

We can describe a spatial pattern whenever patchiness is present in our system, so that it can have a certain amount of predictability and hence it can be described quantitatively (Dale, 1999). The spatial pattern of a tree community in a stand, for example, may occur and be analyzed at more than one scale: local and global scales (Legendre, 1993; Wagner, 2004). Local-scale spatial effects deal with the spatial nature of biotic interactions such as seed dispersal, clonal growth, competition, or patchy environment (i.e., heterogeneous distribution of soil nutrients and moisture availability). These biotic interactions lead to a statistical phenomenon known as spatial autocorrelation (see below). Global-scale spatial effects deal with the spatial structure of the environment in general (i.e., resource gradients), for which some environmental variable displays a spatial dependency on some biotic variable (Manly, 1986; Legendre, 1993; Goreaud et al., 1999; Wagner, 2004).

Spatial analysis applied to a plant community is typically undertaken as a two-step process. First, the analysis needs to give a clear and objective description of whether and on what spatial scale aggregation of plants occurs (the spatial scale over which patterns – or processes- remain constant). Second, it needs to be described how this aggregation alters the interactions between species (Ford and Renshaw, 1984; Dale, 1999; Stoll and Prati, 2001; Turner et al., 2001). Descriptive field observations deal with the first step; however they are unable to link the identified spatial pattern with potential causes (Rees et al., 1996). So far, the quantification of pattern has received considerable attention, but we are still able to quantify better pattern than to understand its underlying causes (Turner et al., 2001). While the detection of a contagious spatial structure confirms that non-random processes are operating, various processes could be contributing to the generation of the observed non-random spatial patterns in any plant population or community (Cale et al., 1989; Wyszomirski et al., 1999). It is important to note that coincidence of spatial patterns and processes does not imply causality, but rather suggests a reason to test for causal mechanisms involved (Turner et al., 2001). However, in a field such as forest ecology, where there might be limited opportunities for large-scale manipulative experiments, descriptive studies still have great potential value and predictive power (Underwood et al., 2000).

1.1.2 Spatial patterns in relation to plant interactions and vegetation dynamics

Local spatial patterns have been shown to correlate with the direction and strengths of plant interaction (Choler et al., 2001; Tirado and Pugnaire, 2003; Kikvidze et al., 2005). In a forest ecosystem, the local spatial structure of individuals plays a key role in the stand dynamics (Duncan and Steward, 1991; Chen and Bradshaw, 1999). These plant interactions generate spatial patterning even under homogeneous environmental conditions (Turner et al., 2001). For instance, the spatial pattern of local competition determines the local environment of each tree, and thus, through competition/facilitation processes, its ability to develop and grow carbon allocation or its probability of dying. Overstory spatial pattern also influences the likelihood of seedling establishment by affecting both seed dispersal and seedbed conditions (Goreaud et al., 1999; He and Duncan, 2000; Goreaud et al., 2002).

During the development of a forest stand, the distribution of trees should reflect the ability of individuals to survive competition and dominate the initial patches (Lorimer et al., 1988; Oliver and Larson, 1996). For example, the spatial pattern established for trees within a patch commonly appears to shift from a clumped to a random distribution with increases in size, probably due to self-thinning (Peet and Christensen, 1987; Kenkel, 1988; Veblen, 1992; Szwagrzyk and Czerwczak, 1993). Barot and Gignoux (2003) stated that an initial and relatively easy way to detect neighborhood effects is to analyze plant spatial patterns. They argued that if a spatial distribution deviates from a random distribution, a neighborhood effect can be hypothesized. Every individual tree modifies its immediate habitat to a greater or lesser extent, and hence influences the habitat for its immediate neighbors. This influence varies through both the individual's life and its demands on the resources of the habitat. The fact that individuals primarily interact with their immediate neighborhood allows us to link the observed patterns to local processes that may be operating on the plant community (Tilman and Kareiva, 1997).

1.1.3 Dealing with the analysis of spatially autocorrelated data

Contrary to experimentation, where sampling may be designed in such a way that observations are independent of each other, ecological data are often autocorrelated (Legendre, 1993; Legendre et al., 2004). Spatial autocorrelation can be simply defined as the correlation of the value of any variable with itself through space. If the values of this variable, at pairs of sites a short distance apart, tend to be more similar than expected for randomly associated pairs of observations, it indicates a positive spatial autocorrelation associated with the variable (Legendre, 1993; Turner et al., 2001). Alternatively, if these values tend to be less similar, we are in the presence of negative spatial autocorrelation (Legendre and Legendre, 1998). When spatial autocorrelation is present, it indicates a lack of independence among observations, which violates one of the key assumptions for using classical statistical tests (Sokal and Rohlf, 1995; Dale, 1999; Keitt et al., 2002). In cases of non-spatial independence, many statistical analyses and inferences may not be appropriate. In particular, if we ignore the non-independence of the observations, then we will likely obtain incorrect and often over-stated probability estimates (Lennon, 2000; Shipley, 2000).

If the observations are spatially autocorrelated, the estimates obtained from the correlation coefficient, ordinary least squares regression (OLS) or analysis of variance (ANOVA) will tend to be biased and over estimate treatment effects. When positive spatial autocorrelation is present at short scales, the use of classical statistical analyses will often lead to correlations, regression coefficients, or differences among groups being significant, when in fact they may not be (high probability of Type I errors) (Cliff and Ord, 1981; Legendre and Fortin, 1989; Legendre, 1993; Legendre and Legendre, 1998; Turner et al., 2001).

1.2 PROJECT OBJECTIVES

In this thesis I will provide empirical evidence that supports the current and potential utility of spatial pattern analyses in forest ecological studies. To this end, my efforts have been directed toward furthering our fundamental understanding about spatial patterns and how these patterns can give us sounder links to the way ecological processes operate and interact at the stand level. My main hypothesis is that spatial patterns of tree and stand dynamics are key to a more complete understanding of the underlying ecological processes. For this research project I worked in managed and natural forest ecosystems, in both the Rocky Mountains of Western Montana, United States, and in Chile (central-south and in Patagonia). In three of the four chapters I worked with ponderosa pine as the dominant species; the other chapter (Chapter 2) was based on Mediterranean *Nothofagus* forests in central-south Chile.

My central proposition is that spatial analysis can help us to better describe the structure of a forest stand and to define more appropriate hypotheses on species coexistence and stand dynamics. This was the main objective of the first study (Chapter 2), where the spatial analysis, based on the Ripley's *L*-function, helped me to better define the ecological role of *Nothofagus glauca* in the Mediterranean ecosystems of central Chile. In the second study (Chapter 3), I worked in a managed uneven-aged ponderosa pine/Douglas-fir stands on the Flathead Indian Reservation, in western Montana. For this investigation, I also made use of the Ripley's *L*-function; however with the main purpose of linking species recruitment composition, spatial associations between different cohorts and different species, to a moisture-level gradient. I used a novel strategy to numerically measure the strength of spatial association. I placed particular interest on whether the degree of spatial association (or disassociation) between saplings and overstory was correlated with relative moisture availability. In the third study (Chapter 4), I worked with ponderosa pine plantations in Patagonia, Chile. The main purpose of this study was three-fold; 1) to evaluate whether a proposed model of stand development occurred similarly in all the sites; 2) to examine the timing and strength of microsite effects relative to competition; and 3) to apply a common geostatistical tool to disentangle microsite effects from competition processes in these young populations. My primary objective in this study was to test a priori hypotheses concerning two different processes (microsite and competition) using a semivariogram approach. Finally, in a fourth study (Chapter 5), I worked in a restoration field experiment at the Lick Creek Area in the Bitterroot National Forest, where ponderosa pine dominates the species composition. For this last chapter, my objective was two-fold: 1) to examine and document the effects of restoration practices on growth, performance and recruitment after the application of treatments; and 2) to evaluate the response of different age classes separately, in particular to more closely assess the response of older trees to restoration treatments. For the latter objective, I developed a spatial ANOVA model that incorporated the spatial autocorrelation in growth and performance among individual trees into the covariance structure of the general ANOVA model. By utilizing this spatial ANOVA model at the individual tree-level, I was able to consider tree age-class as a separate factor in the analysis.

Chapter 2

EFFECTS OF NATURAL AND HUMAN DISTURBANCES ON THE DYNAMICS AND SPATIAL STRUCTURE OF *Nothofagus glauca* (Phil.) Krasser IN SOUTH-CENTRAL CHILE

> "Understanding the distribution, history and ecology of the genus *Nothofagus* is clearly key to understanding the historical plant geography and modern vegetation patterns of the Southern Hemisphere" (Veblen et al., 1996c).

2.1 INTRODUCTION

A general model has been proposed for describing variation in the regeneration dynamics of *Nothofagus* species in southern Chile including disturbance regime, site conditions and the shade-intolerance characteristics of each species (Veblen et al., 1996a; Pollmann and Veblen, 2004). *Nothofagus* species are located either at sites with environmental conditions restrictive for other tree species (high latitudes, high elevations, or edaphically sub-optimal sites) or at more favorable sites with periodic disturbances that vary in magnitude (Veblen and Ashton, 1978; Read and Hill, 1985). Patterns of stand development in Chilean *Nothofagus* forests are relatively well known for the southern area of the country, and are the result of both coarse-scale catastrophic disturbances (primarily mudslides, windstorms and tectonic activity) producing whole-stand replacement and small tree-falls resulting in fine-scale gap dynamics (Donoso, 1993;

Veblen et al., 1996a; Pollmann and Veblen, 2004). In order to improve the representational range of this genus, more evaluation and testing of this general model are needed for the different *Nothofagus* forest types. There is little information, for example, on the diversity of *Nothofagus* forests located at their northernmost distribution in Chile; the Mediterranean zone (Donoso, 1996). We need to know if these forests are a result of catastrophic or chronic disturbances, and understand the nature of competitive relationships between dominant species. For instance, it is unclear if Mediterranean *Nothofagus* species require large disturbances for regeneration, or whether or not it can retain dominance after tree-fall gaps are created.

Among the *Nothofagus* species occurring in the Mediterranean zone of Central Chile, *Nothofagus glauca* is considered one of the dominant tree species (Donoso, 1996). Nonetheless, *N. glauca* has been classified as a vulnerable species (Benoit, 1989) due to the many human-influenced transformations of its habitat conditions, particularly through logging and conversion to *Pinus radiata* plantations (Donoso, 1993). Once again, there is little information on the structure and dynamics of these forests, and therefore it has been difficult so far to develop effective conservation and sustainable management strategies for this species (Donoso, 1996; Litton and Santelices, 1996; Amigo et al., 2000).

Recent work in northern temperate forests emphasizes the key role that spatial structure can play in providing insights to the complex processes of stand establishment and species interactions following disturbances (Ford and Sorrensen, 1992; Tilman and Kareiva, 1997). During the development of a stand, for example, the distribution of trees should reflect the ability of individuals to survive competition and dominate the initial patches (Lorimer et al., 1988; Oliver and Larson, 1996). While it may be difficult to infer ecological processes from these observed spatial patterns (Cale et al., 1989), these data can provide a basis for generating hypotheses about underlying processes (Liebhold and Gurevitch, 2002); such as species coexistence, the quantification of overstory-understory relationships, and the importance of competitive/facilitative interactions. We know for example that mature *N. glauca* forests are richly diverse and include a complex understory structure (Amigo et al., 2000). However, it is unclear how these spatial structures are established or maintained in *N. glauca* forests.

Furthermore, one of the greatest challenges facing ecologists and silviculturists, in general, lies in elucidating and modeling the factors determining vegetation pattern and ecosystem processes of native forests at the landscape scale. One of the first basic pieces of information needed for management and/or conservation of any forest is to determine patterns of forest dynamics and their relation to disturbance agents. Available descriptors of disturbance regimes are only partial and usually deal with a single type of disturbance, i.e., tree-fall or fire (Veblen, 1992). To understand the role of disturbance on the forest dynamics of a specific tree species, the full range of disturbances affecting it should be considered. Quantitative forest structure data relative to disturbance factors affecting *Nothofagus* species dynamics are scant in the Mediterranean zone of south-central Chile.

In this study, I characterized and compared tree composition, structure, and spatial patterns of *Nothofagus glauca* second-growth stands with three contrasting disturbance histories, with the aim of obtaining an understanding of how this species develops under the impact of different disturbance agents, and how its spatial structure (particularly, with other species) can help to better define hypotheses on species coexistence and stand dynamics. The first stand corresponds to a mature stand (120-140 years old); the second stand has developed after logging and fire application (occurred around 20 and 40 years ago); and the third stand developed after catastrophic disturbance (a landslide occurred in 1936). With this variety of disturbance histories, I was interested in answering the following questions: 1) Do *Nothofagus glauca* regeneration dynamics and stand development fit the general model developed for southern *Nothofagus* species? 2) Do these forests have episodic or chronic regeneration patterns? 3) Does the presence of *N. glauca* influence the occurrence of tree and understory species? 4) What is the effect of different disturbance agents on the current composition and structure of these stands? 5) What is the successional status of *N. glauca*?

2.2 METHODS

2.2.1 Study area

The study was carried out in the “Bullileo” sector (36°35’ S, 71°28’ W), San Fabián de Alico, in the southern limit of the Mediterranean-climate zone, which is just north of Ñuble River, Ñuble Province (Region VIII) in the Andean foothills of south-central Chile. This sector also constitutes the southern limit of *N. glauca* (Amigo et al., 2000). This area belongs to the Mesomediterranean belt with per-humid climatic conditions that are characterized by mild winters and dry summers (Donoso, 1996; Amigo and Ramírez, 1998), with almost 80% of the annual precipitation of 1051 mm occurring between May and September. Monthly mean minimum temperatures range from 3.8°C in July to 11°C in January, and monthly mean maximum temperatures range from 12.3°C in July to 28.4°C in January (Estación Meteorológica Universidad de Concepción, Chillán; 180-m a.s.l., and 70 km from the study sites). The soils are shallow with a predominance of volcanic material including andesitic and basaltic materials (Donoso, 1996).

2.2.2 Field methods

Two 0.12-0.14 ha plots were located randomly within each of the three disturbance type sites (hereafter denoted as mature, logged, and landslide sites) where *N. glauca* was the dominant species. The exact locations of the plots were chosen at random within stands that were reasonably accessible. Species nomenclature follows Marticorena & Quezada (1985). I inferred stand development and disturbance history from population age and size structures of the different plots. I also used the spatial location of trees to infer the interactions among species and size-classes.

In each plot all trees greater than 50-cm tall were mapped and measured. The coordinates of the estimated center of each tree and sapling (<5-cm dbh, and taller than 1-m) stem were recorded by a handheld laser range finder (Forest Pro, Laser Technology, Colo., USA) and a digital compass, which estimate the distance and azimuth to the center of each tree (>0.5 m tall) to the nearest 1-mm. The field measurements were converted to coordinates using trigonometric functions. For each mapped tree stem, the species, height and dbh (diameter at 1.35-m above the ground) were measured. Heights were measured with a clinometer. To determine ages, we worked with all the tree cores of one plot per site (Mature site plot 1, and Landslide site plot 2), and more than 50% of the trees in the Logged site plot 1. Tree cores were dried and mounted in grooved wooden boards and sanded with successively finer grades of sand paper to reveal annual rings. Annual rings were hard to read, so we used phloroglucinol to stain rings and used a dissecting microscope to count rings (Patterson, 1961). For cores that missed the pith of the tree, procedures described by Duncan (1989) were used to estimate the number of missing rings. No correction was applied for time required to grow to coring height (20-cm).

I assessed canopy density and projected leaf area index (LAI) for the different plots with fisheye lens canopy digital photographs. Twelve photographs were taken per plot in February 2004 with a 7-mm Nikon f7.4 fish-eye lens, mounted on a Nikon® Coolpix 950-digital camera. The lens has an orthographic projection of 180° angle of view. The camera was mounted 30-cm above the ground on a tripod, leveled and oriented to true north, looking upwards through the canopy. We used the GLA (Gap Light Analyzer V2) software (Frazer et al., 2000) to process the photographs, and to compute percent canopy openings and LAI.

2.2.3 Data analysis

Stand structure was determined from stem diameter and age distributions at each plot. Stem density and basal area (BA) were scaled up to one hectare. For each tree species, a relative importance value (RIV) was computed as an average of the relative density and relative dominance (BA) (Orwig et al., 2001; Pollmann, 2002). Diameters of trees were grouped into 10-cm size classes for *N. glauca* and for all species combined in each plot. Similarity between size- or age-class mean values and distributions of these variables among plots were measured with Mann-Whitney U- and Kolmogorov-Smirnov tests respectively using ranks (Sokal and Rohlf, 1995). Spearman's rank correlation analyses (diameter and age data were not normally distributed –Kolmogorov-Smirnov 1 test) were performed to determine if there were significant correlations between tree diameter and age for *N. glauca*. To test for significant differences among plots for canopy opening and LAI, the data obtained were analysed by a one-way ANOVA; multiple comparisons were conducted using Scheffé's test (Sokal and Rohlf, 1995). The canopy opening values were log-transformed and the LAI values were square-root-transformed to achieve homogeneity of variances. All these analyses were carried out with SPSS (2000).

Shannon's Diversity Index was used to estimate species and structural diversity by grouping species abundance (BA) by height class. Shannon's index, H', is defined as follows:

$$H' = - \sum_{i=1}^{S} pi \times Ln \times pi$$

where p_i is the proportion of individuals in the ith species, S is the number of species (e.g. McCune & Grace (2002)), and Ln is the natural logarithm. This index basically measures the "information content" for a sample unit in terms of uncertainty; the more uncertainty one has about the species of an individual, the higher the diversity of the community. First, we used Shannon's index to estimate species diversity per plot, by accounting for the proportion of *N. glauca* represented as the number of individuals per 2-m height class (p_i). Second, we used Shannon's Diversity Index to estimate structural diversity by using the proportion of basal area per hectare (p_i –relative basal area, RBA) per species (S) (Staudhammer and LeMav, 2001).

2.2.3.1 Spatial pattern analysis

In analysing regeneration processes, it is often useful to account for spatial patterns of trees by mapping individual trees at different scales (Veblen, 1992). Coordinate data (x,y) were collected for every tree to determine the univariate spatial pattern (distribution) for each species, and the bivariate spatial pattern (association) between species and tree-classes at each plot using a modified version of Ripley's *K*-function (Lotwick and Silverman, 1982).

To analyse spatial point patterns, under the assumption of stationarity (the process must be invariant under translation) and isotropy (invariance under rotation), we chose the *L*-function, $L(t) = \sqrt{(K(t)/\pi)} - t$ proposed by (Besag, 1977), which is a linearized version of the Ripley's *K*-function (Ripley, 1977), and is preferred for interpretation. The original Ripley's *K*-function is based on the variance (second-order analysis) of all point to point distances in a two-dimensional space, and gives a description of spatial structure at different scales at the same time (Cressie, 1993). The *L*-function is estimated as: $\hat{L}(t) = \sqrt{(\hat{K}(t)/\pi)} - t$. The *L*-function transformation makes *K(t)* linear in *t* (distance), and scales its variance to facilitate testing against the null hypothesis of complete spatial randomness (CSR; i.e. it is assumed that all points are distributed independently). The linearized function has an expectation of zero for any value of *t* when the pattern is random. The spatial pattern can then be described as clumped, random, or regular at any distance *t* up to about half the length of the shortest rectangular plot side if the calculated $\hat{L}(t)$ is greater, equal or lower than the 99% confidence envelopes, respectively (Dixon, 2002). For this analysis, *N. glauca* individuals were divided into three categories: saplings, juveniles (dbh between 5 and 15-cm), and adults (dbh >15-cm). The statistical significance of the departure of $\hat{L}(t)$ from zero was tested using Monte Carlo-confidence envelopes based on the random repositioning of all points in the plot. In this study, we computed a 99% confidence interval by running 99 simulations at intervals of 1-m from 1 to 16-m (half the length of the shortest side of the plot). The Cramer-von Mises test was used to account for significance (Haase, 2002). Since edge effects become a concern at greater distances, we used weighted edge correction methods to account for this effect (Haase, 1995).

Table 2-1. Site characteristics of each plot sampled at Bullileo location (36°35' S, 71°27'W), San Fabián de Alico, Chile. For canopy opening and projected LAI (leaf area index), the mean and standard error (in parentheses) are presented.

Plots	Altitude (m)	Aspect	Slope (%)	Plot size (m^2)	Canopy opening (%)	LAI (m^2/m^2)	Shannon index*
Mature 1	850	E	40	1200	16.18 (0.67)	2.06 (0.087)	.443
Mature 2	710	NE	15	1200	15.63 (0.84)	2.12 (0.094)	1.189
Logged 1	700	S	12	1400	14.65 (0.91)	2.63 (0.088)	.437
Logged 2	680	S	15	1350	21.09 (1.01)	1.59 (0.078)	.045
Landslide 1	680	S	10	1200	22.67 (0.50)	1.51 (0.036)	.489
Landslide 2	660	S	10	1200	29.92 (1.72)	1.11 (0.088)	.043

* Shannon index was applied for stand structural diversity based on basal area per species.

To estimate the spatial association between species and tree-classes at each plot, we used the bivariate spatial function, $K_{1.2}(t)$ (a derivation of the univariate spatial function), which characterizes the relative location of one type or class (e.g., species or size class 1) with respect to another (class 2). Following the logic used above, we used the modified $L_{1.2}(t)$-function (Lotwick and Silverman, 1982), whose classical estimator is $\hat{L}_{1.2}(t)=\sqrt{(\hat{K}1.2(t)/\pi)-t}$. $\hat{L}_{1.2}(t)$ provides evidence of spatial association between species 1 and 2: if the value of $\hat{L}_{1.2}(t)$ is not significantly different from zero, the null hypothesis that the two species have independent spatial distributions cannot be rejected (Goreaud and Pélissier, 2003). Monte Carlo simulations were used to evaluate the statistical evidence of spatial independence; we built 99% confidence intervals from 99 random shifts of one class of trees with respect to the other. Values of $L_{1.2}(t)$ greater, equal or lower than 99% confidence envelopes indicated significant positive spatial association (attraction) at distance t, spatial independence, and significant negative spatial association (repulsion) between the two tree-classes analysed, respectively (Dixon, 2002; Goreaud and Pélissier, 2003). The spatial statistics program SPPA.EXE (Haase, 2002) was used for both univariate and bivariate spatial analyses.

2.3 RESULTS

2.3.1 Stand structure

All of the *Nothofagus glauca*-dominated study sites have a diverse size structure, particularly for the mature and logged sites. These two sites included abundant saplings, generally with declining numbers of individuals in successively larger diameter classes, exhibiting a negative exponential or reverse-J pattern, typical of uneven-aged forests (Kolmogorov-Smirnov 1-sample test; Fig. 2.1a and 2.1c). For instance, in the mature site, stems <5-cm dbh accounted for ca. 46 and 76% of the plot 1 and 2 populations, respectively. In contrast, the two plots from the landslide site exhibited a normal-shape diameter distribution, accounting for ca. 42 and 79% of their stems in middle size-classes (9.5-15-cm dbh), for landslide site plots 1 and 2, respectively (Kolmogorov-Smirnov 1-sample test; Fig. 2.1b). Age-DBH relationships were highly significant for all three sites (R^2=0.93, 0.73 and 0.67 for mature, logged and landslide sites, respectively; ***results not shown***). Hence, I considered size data sufficient to explain stand structure for all the sites. Donoso et al. (1984) and Veblen (1985) found highly correlated age-DBH relationships for temperate rain forests. Across the different sites, *N. glauca* also represented an all-aged population, forming the oldest tree-cohorts; recruited ca. 1860 (mature site plot 1), 1880 (mature site plot 2), 1960 (logged site plot 1), 1987 (logged site plot 2), and 1940 (landslide site). The basal area across most of the study sites was moderate (21.4-37.8 m^2/ha), and low for the logged site plot 2 and the landslide site plot 2 (9.34 and 14.3 m^2/ha, respectively).

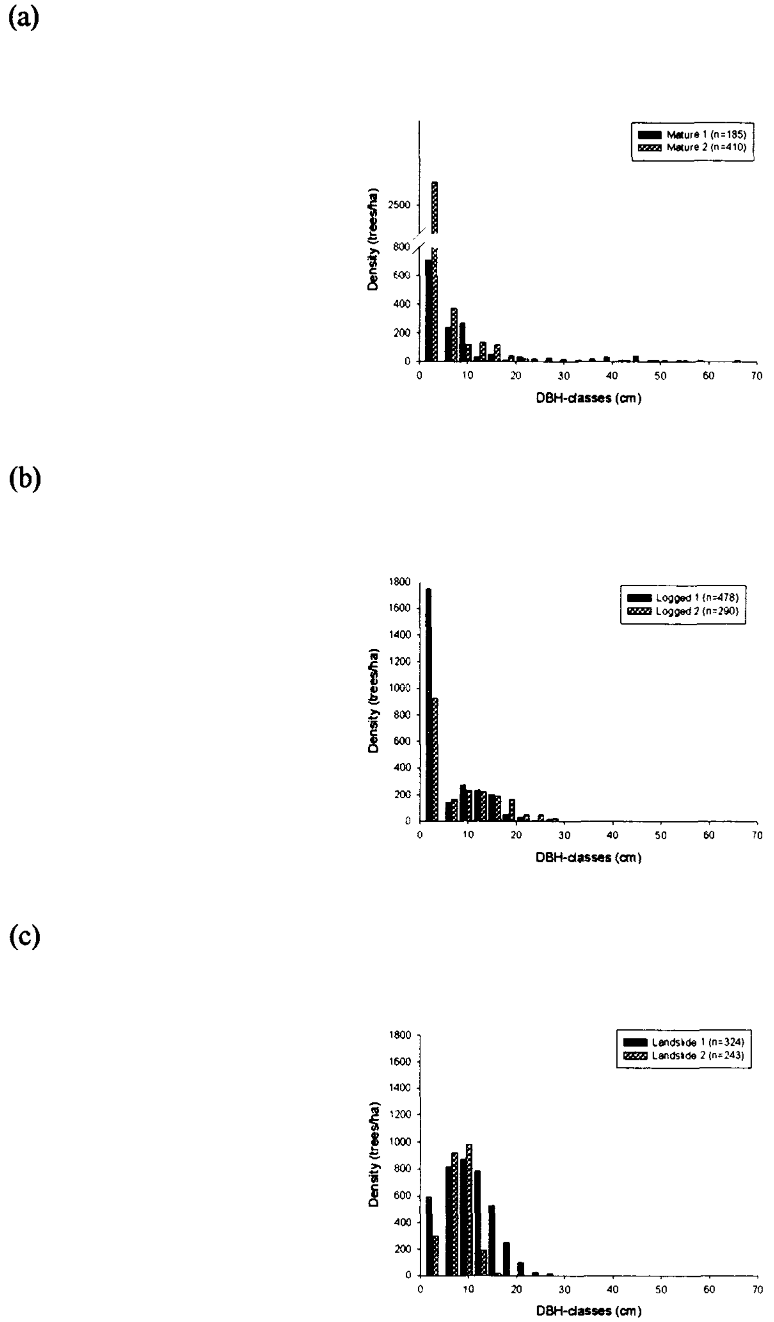


Figure 2-1. Diameter size class frequency distribution for the three sites; a) mature stand; b) logged stand; and c) landslide stand, in Bullileo sector, San Fabián de Alico, Chile.

Table 2-2. Density (trees/ha), basal area (m^2/ha), relative density (RD), and relative basal area (RBA) for trees larger than 5-cm dbh, for all the plots in Bullileo sector, San Fabián de Alico, Chile. Relative importance values (RIV) were calculated as: (relative density + relative basal area)/2.

Plot	Density	RD	Basal Area	RBA	RIV
mature 1					
N. glauca	850	88.7	29.3	88.5	88.6
N. obliqua	8.3	0.1	1.1	3.3	1.7
N. leoni	16.7	1.7	2.4	7.3	4.5
G. avellana	66.7	7.0	0.2	0.6	3.8
A. serrata	8.3	0.1	0.02	0.1	0.1
P. lingue	8.3	0.1	0.02	0.1	0.1
Totals	958		33.1		
mature 2					
N. glauca	841.7	49.7	13.8	64.6	57.2
N. obliqua	100	5.9	3.5	16.4	11.1
N. leoni	66.7	3.9	0.7	3.3	3.6
G. avellana	241.7	14.3	0.9	4.2	9.2
A. serrata	91.7	5.4	0.3	1.4	3.4
P. lingue	25	1.5	0.2	0.9	1.2
C. alba	266.7	15.8	1.7	8.0	11.9
L. dentata	41.7	2.5	0.2	0.9	1.7
A. punctatum	16.7	1.0	0.06	0.3	0.6
Totals	1692		21.4		
logged 1					
N. glauca	2957.1	88.8	32.4	85.8	87.3
G. avellana	321.4	9.7	5.1	13.6	11.6
A. serrata	50.0	1.5	0.3	0.7	1.1
Totals	3329		37.8		
logged 2					
N. glauca	1770	99.2	9.3	99.3	99.2
G. avellana	7	0.4	0.01	0.1	0.3
A. serrata	7	0.4	0.05	0.6	0.5
Totals	1784		9.34		
landslide 1					
N. glauca	1308	77	21.0	88.2	82.6
G. avellana	208	12.3	1.7	7.2	9.7
L. caustica	58	3.4	0.2	1.0	2.2
L. hirsuta	100	5.9	0.6	2.7	4.2
L. dentata	18	1.0	0.2	0.8	0.8
C. alba	8	0.4	0.02	0.1	0.2
Totals	1700		23.72		
landslide 2					
N. glauca	1083	95.0	13.6	99.2	97.1
A. chilensis	8.3	5.0	0.7	0.7	2.9
Totals	1092		14.3		

2.3.2 Stand composition

At all three study sites, *N. glauca* was the dominant tree species (highest RIV, Table 2.2). At sapling level, *N. glauca* had densities of 300-2042 saplings/ha (relative densities of 17.9-48.9%; Table 2.3). Plant species composition was markedly different among the study sites, especially for saplings (Fig. 2.2). Within the tree stratum, the mature site plot 2 exhibited the greatest overall diversity, particularly for shade-tolerant species (highest Shannon's Diversity index (1.7), Table 2.1 and 2.2). *Gevuina avellana* was well represented in the mature sites, logged site plot 1, and landslide site plot 1 (RIV of 4.5, 9.2, 11.6, and 9.7%, respectively); *Cryptocaria alba* had the highest RIV (11.9%) after *N. glauca* in mature site plot 2 (Table 2.2). The landslide site presented the lower diversity for the tree stratum (Shannon's Diversity index = 0.043). At the tree sapling-shrub stratum, *Azara serrata*, *Pernettya mucronata*, and *Sophora macrocarpa* dominated in the mature site plot 1; *G. avellana*, *Sophora mayu*, and *Chusquea cumingii* dominated the mature site plot 2. For the logged site plot 1, the most frequent saplings were *G. avellana* and *A. serrata*, and for the logged site plot 2, *S. mayu*, *Baccharis confertifolia*, and *Lithraea caustica* were the most common. *B. confertifolia* and *L. caustica* dominated the shrub layer in the landslide site (Table 2.2).

2.3.3 Canopy structure

The logged site plot 1 had a significantly lower canopy opening (14.65%) and higher projected LAI (2.63 m^2/m^2) when compared with the rest of the sites ($p<0.005$, Table 2.1 vs. Table 2.4). The opposite was found for the landslide site plot 2; a significantly higher canopy opening (29.92%) and lower projected LAI (1.11 m^2/m^2; Table 2.1) than the rest of the sites ($p<0.01$; Table 2.4). At the other sites (mature and logged) there were no significant differences in canopy structure within a site, but between these two sites we found a significant difference in canopy opening and projected LAI. The upper canopy layer was dominated by *N. glauca* for most of the sites (*N. obliqua* for the mature site plot 2), achieving maximum heights in the mature site plot 1 of ca. 19-m. These heights are below the maximum heights documented by Donoso (1996), which are close to 30-m. The Mature site plot 2 presented the highest structural diversity (highest Shannon's values through height -Fig. 2.2), while the Logged site had the lowest values.

Table 2-3. Saplings (>1-m tall and <5-cm dbh) abundance (stems per hectare) within study sites in Bullileo sector, San Fabián de Alico, Chile. Values in parentheses are relative densities.

Species	mature 1	mature 2	logged 1	logged 2	landslide 1	landslide 2
Nothofagus glauca	2042 (43.0)	1108 (17.9)	614.3 (29.4)	2160.3 (48.9)	591.7 (18)	300 (22.5)
Nothofagus obliqua		50 (0.8)				
Nothofagus leonii		66.7 (1.1)				
Gevuina avellana	333.3 (7.0)	541.7 (8.8)	635.7 (30.4)	223 (5.1)	300 (9.1)	
Azara serrata	491.7 (10.4)	166.7 (2.7)	535.7 (25.6)	369.3 (8.4)	108.3 (3.3)	50 (3.8)
Pernettya mucronata	558.3 (11.8)					
Cryptocaria alba		91.7 (1.5)				8.3 (0.6)
Lomatia dentata	75 (1.6)	25 (0.4)	64.3 (3.1)			
Bacharis spp.	141.7 (3.0)				691.7 (21)	208 (15.6)
Sophora mayu	741.7 (15.6)	391.7 (6.3)	128.6 (6.1)	1351.9 (30.6)	450 (13.7)	258 (19.4)
Chusquea cumingii	341.7 (7.1)	3692 (59.8)		139.4 (3.2)	16.7 (0.5)	
Persea lingue	25 (0.5)					
Luma apiculata		8.3 (0.1)				
Lithraea caustica		16.7 (0.3)	14.3 (0.7)	41.8 (1.0)	866.7 (26.3)	450 (33.7)
Maytenus boaria		16.7 (0.3)				
Lomatia hirsuta			92.9 (4.4)	132.4 (3.0)	258.3 (7.9)	50 (3.8)
Quillaja saponaria						8.3 (0.6)
Aristotelia chilensis			7.1 (0.3)			
Austrocedrus chilensis					8.3 (0.3)	
Total	4750	6175	2092.9	4418	3292	1333

2.3.4 Spatial pattern distributions and associations

The spatial distribution of *N. glauca* tree stems differed by size classes in most of the sites (Table 2.5), displaying mostly random spatial distributions for trees larger than 15-cm dbh. The logged site plot 1, however, resulted in a clumped spatial distribution through all *N. glauca* size classes. For smaller dbh classes (5 and 15-cm) and saplings, the spatial distribution was significantly clumped for most distance classes ($p<0.01$). Companion species showed significant clumpiness across all distance classes for both trees and saplings. Overall, I found strong evidence for a positive association between saplings and adult trees of *N. glauca* belonging to the dbh class 5-15-cm. For overstory trees larger than 15-cm dbh, the association pattern is not clear, having some positive association at larger scales; near 10-m for the mature site plot 2, logged site plot 1, and landslide site, respectively (Table 2.6). At the mature site plot 2, both adult trees and saplings of *N. glauca* were independently associated with *N. obliqua* and *N. leoni* ($p>0.05$).

The predominant companion species were *G. avellana* and *C. alba*, which exhibited negative spatial associations with all the size classes of *N. glauca* ($p<0.01$; Table 2.6) at the mature plot 2, logged site plot 1, and landslide site plot 1 (*G. avellana*), and mature site plot 2 (*C. alba*). At the mature site plot 1, I found that the bamboo species *C. cumingii* was negatively associated with saplings of *N. glauca* only ($p<0.01$; Table 6), while *P. mucronata* was negatively associated with adult trees of *N. glauca* ($p<0.01$), but not with saplings. I also found that saplings of *G. avellana* were positively associated with adult trees of *N. glauca* ($p<0.01$), but negatively associated with its saplings ($p<0.01$). At the mature site plot 2, the spatial association of *C. cumingii* with *N. glauca* trees of 5-15-cm dbh and saplings was negative at all distances ($p<0.01$; Table 6), but positive in the first 6-m when compared with adult trees larger than 15-cm dbh ($p<0.01$). Finally, at the landslide site plot 2, I found that *L. caustica* had a negative spatial association with *N. glauca* saplings (p<0.01), and no spatial association with adult trees of *N. glauca* (p>0.05; Table 6).

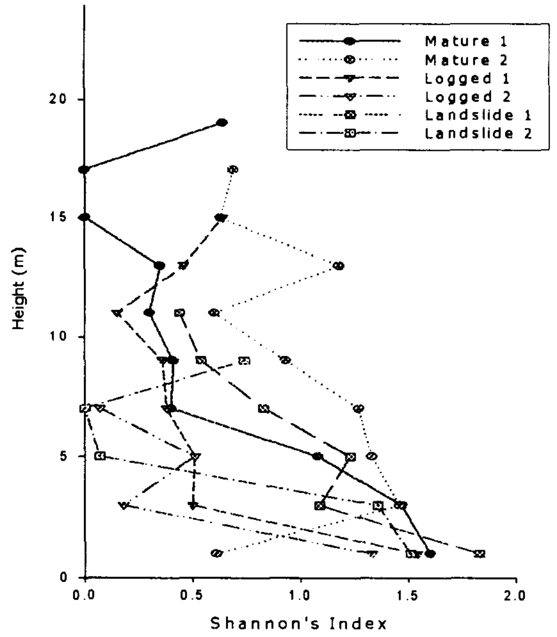


Figure 2-2. Relationship between Shannon's Diversity index for species diversity by height class using species abundance data across all the *Nothofagus glauca* stands at Bullileo sector, San Fabián de Alico, Chile.

2.4 DISCUSSION

Like many other mesophytic temperate forest ecosystems, *Nothofagus* forests in southern Chile are often products of large disturbance events, including landslides, mudslides, windstorms, and fire (Veblen and Ashton, 1978; Veblen et al., 1996a; Pollmann and Veblen, 2004). By contrast, some *Nothofagus* species (e.g. *N. antarctica*, *N. nitida*, *N. pumilio*) located in harsh habitats, subalpine or wet microsites tend to exhibit greater adaptations towards gap replacement (Rebertus and Veblen, 1993; Fajardo and de Graaf, 2004; Gutiérrez et al., 2004). *Nothofagus glauca*-dominated forests, as reported here, develop in a distinctive manner since they typically retain open patchy canopies even more than 140 years following disturbance. *Nothofagus glauca* had population structures indicative of continual recruitment across the oldest study site, constituting a steady-state population (Veblen, 1992). In addition, I found that the most diverse structure and species composition occurred in this oldest site. All of these factors together suggest that *N. glauca*, even under good growing conditions, is growing in such a tough moisture limited environment that it is behaving like southern *Nothofagus* species growing on the most marginal of site conditions.

Table 2-4. Differences between (Log transformed) canopy opening (above the squares) and projected (square root transformed) LAI (leaf area index, below squares) based on Scheffé multiple comparison significance values among the plots. Bold figures indicate significant differences ($p<0.05$).

Plots	mature 1	mature 2	logged 1	logged 2	landslide 1	landslide 2
mature 1		-.018	**.106**	**.114**	**.149**	**.264**
mature 2	.020		**.123**	**.132**	**.167**	**.282**
logged 1	**.159**	**.179**		.008	.044	**.158**
logged 2	**.173**	**.193**	.014		.035	**.150**
landslide 1	**.204**	**.224**	.045	.031		**.115**
landslide 2	**.387**	**.406**	**.228**	**.213**	**.183**	

2.4.1 Mature stand; composition, structure, and succession

While the mature site was sufficiently open to allow regeneration throughout the stand it nevertheless showed a strong pattern of clumping of saplings. Various processes can lead to a clumped pattern of the youngest cohorts. For example, natural or mechanical soil disturbances may create patches of favorable seedbed; proximity to seed source or obstructions to seed movement, or patches of increased resource availability as might be associated with canopy gaps (Veblen, 1992; Franklin et al., 2002). The pattern of sapling clumps in the sites is consistent with models of canopy-gap or patch dynamics stand development (Pickett and White, 1985; Peet and Christensen, 1987).

Table 2-5. Patterns of spatial distributions based on the univariate L-function for tree-classes of *N. glauca* and a group of companion species through all the study sites in Bullileo sector, San Fabián de Alico, Chile.

Plots	n	*N. glauca*, dbh > 15-cm Distance t (m)* 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	p†
mature 1	33																0.720
mature 2	23																0.289
logged 1	87	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 2	1	=	=	=	=	=	=	=	=	=	=	=	=	=	=	=	
landslide 1	53																0.220
landslide 2	31																0.981

Plots	n	*N. glauca*, dbh 5 - 15-cm Distance t (m) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	p
mature 1	65	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
mature 2	78	c	c	c	c	c	c	c	c	c	c	c	c	c	c		**0.001**
logged 1	325	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 2	254	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
landslide 1	104	c	c	c	c	c	c	c	c	c	c	c	c	c	c		**0.001**
landslide 2	102	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**

Plots	n	Companion species, dbh > 5-cm Distance t (m) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	p
mature 1	103	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
mature 2	160	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 1	62	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 2	0	=	=	=	=	=	=	=	=	=	=	=	=	=	=	=	
landslide 1	45	c	c	c	c	c	c	c	c	c			c	c	c	c	**0.001**
landslide 2	54	c	c	c	c	c	c	c	c	c	c	c	c		c	c	**0.002**

Plots	n	*N. glauca* saplings, dbh < 5-cm Distance t (m) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	p
mature 1	244	c	c	c	c	c	c	c	c	c	c	c	c				**0.001**
mature 2	131	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 1	83	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 2	310	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
landslide 1	70	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
landslide 2	34	c	c	c	c	c	c	c	c			c	c	c	c	c	0.013

Plots	n	Understory species, dbh > 5-cm Distance t (m) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	p
mature 1	108	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
mature 2	463	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 1	202	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
logged 2	277	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
landslide 1	324	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
landslide 2	61	c	c	c	c	c	c	c	c	c	c						**0.001**

* The symbol *c* indicates a significant clumped distribution; *u* means a regular distribution at distance *t*, based on the *L(t)*-function values distribution. An empty cell indicates a random distribution (= means not applicable).

† Significance is using a 99% confidence interval (999 simulations) with a 1-m step. The Cramer-von-Mises test was used for overall significance of patterns over the complete range of t. Bold figures mean the spatial dispersion is highly significant at the 0.01 level.

The oldest site had the most open canopy of all the study sites (lowest LAI and highest percent canopy opening values), so that the presence of discrete gaps was rather difficult to define (Lieberman et al., 1989) and therefore might not be the principal cause of regeneration patchiness. Regarding the other processes, proximity to seed sources (seed shadow) might be a plausible cause for regeneration clumpiness, since seeds of this species appear to have limited mobility (largest seed size in the genus, 2000 seeds/kg, (Donoso, 1996)), and therefore dispersal can be confined to spots near parent trees. However, positive spatial associations between saplings and larger trees (>15-cm dbh) were not found, at least not at closer distances (<10-m). The presence of *Chusquea* (C. *cumingii* Nees) might also play a role in regeneration patchiness, in as much as it has been reported to effect the rate, timing, and composition of tree regeneration in tree-fall gaps, particularly in Southern Chile *Nothofagus* forests (González et al., 2002; Fajardo and de Graaf, 2004). The negative spatial association between *N. glauca* saplings and the bamboo species may reflect competition processes, which have developed in niche differentiation displayed by the spatial patterns observed. It is not clear, however, what the competition source would be. Further studies on resource partitioning and niche differentiation between *N. glauca* regeneration and *C. cumingii* are needed, since these bamboo can become a threat for successful regeneration in *Nothofagus* forests (Veblen et al., 1996a; González et al., 2002).

Mature stands of *N. glauca* have been reported to have open canopies with large gaps, which may explain their rich and diverse multi-layered understory (Amigo et al., 2000). Companion species, particularly shade-tolerant species, were more abundant in this site than in the rest. The presence of *C. alba*, a shade tolerant species (Chacón and Bustamante, 2001), as well as *P. lingue* and *A. punctatum*, and the facultative shade-tolerant *G. avellana* (Figueroa and Lusk, 2001), could suggest a shift from shade-intolerant to shade-tolerant tree species dominance. Studies in mixed forests have shown that shade-intolerant *Nothofagus* species do not regenerate in undisturbed old-growth forests (Veblen et al., 1981; Pollmann, 2002). Nonetheless, along with what Pollmann (2002) has already suggested for *N. alpina*, the presence of tree-fall gaps (with reduced competitive effects), in general, along with increased light levels (high canopy openings), in particular for this study site, may be responsible for the continuous recruitment of *N. glauca*. On the other hand, there was not a clear spatial pattern when these species were compared with *N. glauca* size classes; positive association in mature site plot 1 for *G. avellana* and negative in mature site plot 2 for *G. avellana* and *C. alba*. These spatial patterns may be indicative of a mix of ecological factors influencing these patterns including species ecological tolerance, historical factors and/or biotic interactions.

The spatial pattern established for *N. glauca* trees appeared to shift from clumped to a random distribution with increases in size (hence age). This pattern is consistent with the interpretation that stand development consists of episodic tree establishment in small groups followed by self-thinning (Peet and Christensen, 1987). This pattern is in accordance with what Fajardo & de Graaf (2004) reported for *N. pumilio* stands in two different localities of southern Chile, and for many other temperate forests around the world (Kenkel, 1988; Read and Hill, 1988; Stoll et al., 1994; Mast and Veblen, 1999). The large variety of horizontal and vertical structures within the stand is also consistent with a history of continuous recruitment.

2.4.2 Effects of disturbances on stand structure and dynamics

In the logged site it is clear that *N. glauca* is following a catastrophic regeneration mode with vigorous young trees of similar age showing evidence of competitive interactions and lower rates of regeneration (Veblen, 1992; Oliver and Larson, 1996). Human-disturbances in *N. glauca* stands have been occurring primarily in the form of clearing forest patches of one to three hectares. The timber is cut for charcoal, and debris is burned (a term locally called "*roce*"). Later, the site is abandoned and forest succession proceeds. If the logging has not created serious soil disturbances, *N. glauca* vigorously re-sprouts from stumps (Donoso, 1993), and forms a dense even-aged second-growth stand. The sprouting nature might be the explanation for a significant clumped distribution among the size-classes of *N. glauca* at this site.

Historically speaking, the disturbance-regeneration model just depicted is the one applicable to our study site. Litton & Santelices (2002) have also corroborated this disturbance-regeneration model for the Coastal range. However, San Martín & Donoso (1997) noted that anthropogenic degradation of *N. glauca* in the Coastal range can produce local shifts to dominance by sclerophyllous species, and more severe disturbances have resulted in invasions by exotic shrubs that often prevent forest regeneration. An intriguing, but as yet untested hypothesis is that these disparate responses to human disturbance might be influenced by the size and degree of fragmentation of the landscapes within which these stands occur (perhaps, at larger scale, between the Coastal and the Andean range).

The landslide study site provides an interesting contrast in response to disturbance, since, although older than the Logged site, it still represents an early successional state and a stem initiation stand development phase, after Oliver's model (Oliver and Larson, 1996). It also followed a catastrophic regeneration mode (Veblen, 1992); where *N. glauca* is the dominant species and there is continuous recruitment. Hence, the particular nature and intensity of the disturbance make this site appear structurally different from the Logged site. LAI and BA are much lower than in the logged site. These stand characteristics along with the presence of extremely rocky soil (*personal observations*) lead to a prediction of low stand productivity. The landslide occurred in 1936, and since then there have been pulses of regeneration of *N. glauca*, followed by other shade-intolerant sclerophyllous species like *L. caustica* (Anacardiaceae) and *L. hirsuta* (Proteaceae). All these characteristics provide evidence that *N. glauca* is a pioneer and a shade-intolerant tree species. A prompt colonization of *Nothofagus* species after catastrophic disturbances has commonly been reported to occur in Southern Chile and Argentina; including *N. alpina* in the Malleco province (Pollmann, 2002), and *N pumilio* in Tierra del Fuego (Rebertus and Veblen, 1993). *Nothofagus glauca* has many unique morphological adaptations to help deal with high temperatures and droughty soils in these extreme environments including thick bark and tough coriaceous leaves (Donoso, 1996; Ramírez et al., 1997), providing an advantage over other *Nothofagus* species in the area (i.e., *N. obliqua*).

Saplings were mainly associated with adult trees, likely due to the harsh characteristics of the site, even though *N. glauca* is a shade-intolerant tree species. In this moisture-limited site we might expect to see a reduced spatial association between regeneration and canopy openings since canopy openings might be less hospitable to new germinants because of excessive temperatures and moisture stress. Some authors have argued that on more xeric habitats, reduced moisture stress under adult tree canopies may explain the increased sapling abundance beneath their canopies (Callaway, 1992; Bertness and Callaway, 1994). This positive spatial association may result from a facilitative relationship of larger "nurse plants" providing shelter to seedlings by buffering physical stresses, especially high temperature. Bertness & Callaway (1994) suggested that facilitation could potentially play a more important role than competition in resource-limited environments.

2.5 CONCLUSIONS

In comparison with studies on dense *Nothofagus* rain forests in southern Chile, this study suggests that the regeneration of *N. glauca* is not necessarily dependent on large disturbances. Low canopy density allowed for diverse understory species in all sites. These findings support the model of *Nothofagus* regeneration dynamics, which states that *Nothofagus* species occur in sites experiencing coarse-scale disturbances and/or in harsh site conditions (for its potential competitors). *Nothofagus glauca* can be both a pioneer on harsh sites as well as a gap strategist in mature forests. In these harsh sites the greatest amount of species, the densest canopies and the most diverse structures occur in the oldest forests.

According to Amigo et al. (2000), the sites under study belong to the *Bomareo-Nothofagetum glaucae* phytosociological association. In this association *N. glauca* is the dominant tree species, and the presence of companion tree species will depend on the water availability status of the area (Donoso, 1996). I found that *N. glauca* occurred with some tree species belonging to the Mediterranean sclerophyll forest, such as *C. alba*, *L. caustica,* and *Q. saponaria* (landslide site), but also found *N. glauca* accompanied by tree species more characteristic of southern Chilean rain forests such as *A. punctatum* (mature site). The wide variety of plant associations in a small geographic area provides evidence of the transitional nature of vegetation characteristics in this zone (San Martín and Donoso, 1997).

Table 2-6. Patterns of specific spatial association based on the bivariate $L_{1,2}$-function between *N. glauca* size-classes and species through all the study sites in Bullileo sector, San Fabián de Alico, Chile.

Sites		Distance t (m)															
Mature 1	n_1/n_2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	p
N.g. >15 vs. *N.g.* saplings	33/244			-						-	-			-			0.024
N.g. 5-15 vs. *N.g.* saplings	65/244									-	-						0.053
N.g. >15 vs. *C. cumingii*	33/38		+			+	+										0.339
N.g. >15 vs. *P. mucronata*	33/70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. >15 vs. *G. avellana*	33/49	+	+	+	+	+	+	+	+	+	+	+	+	+			**0.002**
N.g. >15 vs. *C. alba*	33/92																0.768
N.g. 5-15 vs. *C. cumingii*	65/38																0.888
N.g. 5-15 vs. *P. mucronata*	65/70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. 5-15 vs. *G. avellana*	65/49	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. 5-15 vs. *C. alba*	65/92																0.076
N.g. saplings vs. *C. cumingii*	244/38	-	-	-	-	-	-	-	-								**0.009**
N.g. saplings vs. *P. mucronata*	244/70													+	+	+	0.011
N.g. saplings vs. *G. avellana*	244/49			-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. saplings vs. *C. alba*	244/92	+	+														0.295
Mature 2																	
N.g. >15 vs. *N.g.* saplings	23/131													+	+	+	**0.007**
N.g. 5-15 vs. *N.g.* saplings	78/131	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. >15 vs. *N. obliqua*	23/15																0.506
N.g. >15 vs. *N. leoni*	23/16				-								+				0.283
N.g. >15 vs. *C. cumingii*	23/416	+	+	+	+	+	+										**0.001**
N.g. >15 vs. *G. avellana*	23/87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. >15 vs. *C. alba*	23/42				-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. 5-15 vs. *N. obliqua*	78/15																0.460
N.g. 5-15 vs. *N. leoni*	78/16																0.515
N.g. 5-15 vs. *C. cumingii*	78/416	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. 5-15 vs. *G. avellana*	78/87				-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. 5-15 vs. *C. alba*	78/42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. saplings vs. *N. obliqua*	131/15																0.726
N.g. saplings vs. *N. leoni*	131/16																0.585
N.g. saplings vs. *C. cumingii*	131/416	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. saplings vs. *G. avellana*	131/87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. saplings vs. *C. alba*	131/42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
Logged 1																	
N.g. >15 vs. *N.g.* saplings	87/83									+	+	+	+	+	+	+	**0.002**
N.g. 5-15 vs. *N.g.* saplings	325/83	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. >15 vs. *G. avellana*	87/45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.004**
N.g. 5-15 vs. *G. avellana*	325/45		-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.012
N.g. saplings vs. *G. avellana*	83/45		-	-	-	-				-	-	-	-	-	-	-	0.020
Logged 2																	
N.g. 5-15 vs. *N.g.* saplings	254/310	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. 5-15 vs. understory	254/324	+	+	+	+	+	+										0.093
Landslide 1																	
N.g. >15 vs. *N.g.* saplings	53/70													+	+	+	**0.002**
N.g. 5-15 vs. *N.g.* saplings	104/70	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. >15 vs. *G. avellana*	53/26				-		-						-	-	-	-	0.412
N.g. 5-15 vs. *G. avellana*	104/26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
N.g. saplings vs. *G. avellana*	70/26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.001**
Landslide 2																	
N.g. >15 vs. *N.g.* saplings	31/34										+	+	+	+	+	+	**0.003**
N.g. 5-15 vs. *N.g.* saplings	102/34	+	+														0.246
N.g. >15 vs. *L. caustica*	31/56																0.056
N.g. 5-15 vs. *L. caustica*	102/56																0.944
N.g. saplings vs. *L. caustica*	36/56					-	-	-	-								**0.004**

* The symbol + means a significant positive association; - means a significant negative association at distance t, based on the $L_{1,2}(t)$-function. An empty cell indicates an independent association. Significance is using a 99% confidence interval (999 simulations) with a 1-m step. The Cramer-von-Mises test was used for overall significance of patterns over the complete range of t. Bold figures mean the spatial association is highly significant at the 0.01 level.

Basal area and density values differed according to site, obviously due to different stand development stages. Maximum BA values were found in the second-growth stand following logging (logged site plot 1: 37.8 m^2/ha) and in the mature stands (mature site plot 1: 33.1 m^2/ha). *Nothofagus glauca* has lower BA values when compared with other *Nothofagus* species of southern Chile; Pollmann (2002), working in the Malleco Province (38° 13'S), found maximum BA values of 110 m^2/ha for *N. alpina*. In old growth stands of *N. pumilio*, Fajardo & de Graaf (2004) found BA values of 68 and 61.9 m^2/ha in sites located in the Ñuble Province (36° 60'S) and the Coyhaique Province (45° 52'S), respectively. The data suggest that the productivity levels of these *N. glauca* stands are well below *Nothofagus* species located in southern Chile. I suggest that Mediterranean climatic conditions, characterized by long droughts plus thin rocky soils (in the current study), in contrast to wet climates in the south, explain these low productivity rates (Kalin-Arroyo et al., 1995; Mooney et al., 2001).

The current study gives preliminary information on this particular *Nothofagus* forest type. Further studies on the links between regeneration behavior, primary productivity, nutrient cycles and ecophysiology for these three origin disturbance stands are needed (Veblen et al., 1996a). Another important field of study to explore is the landscape connectivity that these Andean foothills share with the fragmented forests of the Coastal range. Finally, I want to add that extensive stand degradation and decreasing range size are serious concerns for *N. glauca*. Based on this work, effective conservation of this species must include both an understanding of the landscape context and the spatial pattern of associated species.

Chapter 3

SPATIAL PATTERNS OF REGENERATION IN MANAGED UNEVEN-AGED PODEROSA PINE/DOUGLAS-FIR FOREST OF WESTERN MONTANA

> "... critical tests of logically derived hypotheses about ecological patterns are valid as experimental science, including studies that are observational (or mensurative) rather than manipulative" (Underwood et al., 2000)

3.1 INTRODUCTION

The two-dimensional spatial pattern of individual trees in a stand can influence competition levels, growth rates, and understory development (Duncan and Steward, 1991; Chen and Bradshaw, 1999; Goreaud et al., 1999). The establishment, development and composition of recruitment is determined in large part by the spatial pattern of larger trees, along with the variation in biophysical site factors, particularly in natural ecosystems (Duncan, 1991; Haase et al., 1996; Goreaud et al., 1999; Mast and Veblen, 1999; Szwagrzyk et al., 2001). Furthermore, studies based on local spatial association patterns have shown correlations with the direction and strength of plant interactions, giving insight into processes such as the nurse effects and niche limitations (Choler et al., 2001; Kikvidze et al., 2005). In this context, spatial patterns can be studied as a means of inferring explanations of interspecific processes (MacArthur, 1972), given that ecological processes may be expected to give rise to spatially recognizable structures that can be examined with spatial statistical analysis (Watt, 1947; Greig-Smith, 1979; Kikvidze et al., 2005; Stoll and Bergius, 2005).

Spatial patterns of forest regeneration are the result of seed dispersal, seed germination, and seedling survival in relation to the distribution of parent trees, competing vegetation, and seedbed conditions. These interactions are in turn affected by disturbances and environmental variables across a range of scales (Nathan and Muller-Landau, 2000). In forest types where small-scale disturbances predominate, the recruitment of young trees into the overstory can occur primarily within canopy openings (Runkle, 1981). Such canopy gap disturbances often result in patches of similar-aged trees, though more variable-aged cohorts of advanced regeneration may be released in many forest types (Brokaw, 1985; Uhl et al., 1988; McClure et al., 2000; Webster and Lorimer, 2005). The size and spatial configuration of canopy openings have long been reported to potentially influence both the amount and species composition of regeneration, particularly for more light-demanding tree species in mesic forests (Minckler and Woerheide, 1965; Brokaw, 1985; Gray and Spies, 1996; Fajardo and de Graaf, 2004). In moisture-limited forests, however, the spatial pattern of regeneration might not be as clearly associated with canopy openings, particularly if establishment of new germinants is facilitated by the greater moisture availability under larger nurse plants (Niering et al., 1963; Callaway, 1992).

In recent years, there has been increased interest in the application of uneven-aged silvicultural systems (both single-tree and group selection) in western North American forests (Fiedler et al., 1988; Guldin, 1996; O'Hara, 1996), particularly in lower elevation ponderosa pine (*Pinus ponderosa* Dougl.) and Douglas-fir (*Pseudotsuga menziesii* var.

glauca (Mirbel) Franco) forests. Uneven-aged management can pose difficult silvicultural challenges, however, in part because selection harvests must consider both the recruitment of a new age class and the maintenance of vigorous growth on the reserve growing stock (i.e., the older cohorts). While identifying suitable allocation of growing space among different age cohorts to meet both considerations remains an active area of silvicultural research (O'Hara, 1996; Seymour and Kenefic, 2002), few studies have considered the actual spatial distribution of trees in different cohorts (Woodall, 2000; Kunstler et al., 2004; Rock et al., 2004; Paluch, 2005). Under the single-tree selection system, managers emulate natural gap phase replacement and implicitly consider the spatial structure of a stand by assuming that canopy gaps constitute potential growing space for new cohorts (Smith et al., 1997; Nyland, 2002). However, it is unclear to what extent regeneration occurs in clumps in managed ponderosa pine/Douglas-fir forests, and whether these two species tend to occur together or in separate microsites. Under low reserve basal area on moisture-limited sites within these forests, the spatial pattern of regeneration may not be as clearly associated with canopy openings. Previous studies in natural ponderosa pine stands have indicated that younger trees tend to be clumped, while larger trees tend to become more randomly dispersed over time (Cooper, 1961; Harrod et al., 1999; Mast and Veblen, 1999; Woodall, 2000).

While point pattern analyses (Dale, 1999) of a single species or bivariate spatial analyses between different groups do not directly identify causal factors involved in stand dynamic processes, they could enhance our understanding of competitive and spatial relationships among different tree species and age classes. Moreover, such analyses of spatial patterns may be used to identify possible underlying processes and to generate hypotheses (Szwagrzyk, 1990; Legendre, 1993; Liebhold and Gurevitch, 2002). For instance, a positive spatial association between two species may suggest that they share similar environmental site requirements, or that the species are somehow dependently linked to each other. Alternatively, a negative association may imply that one species is excluding the other (Dale, 1999), or that the species may differ in resource use, dispersal and germination mechanisms, or reproductive strategies (Bazzaz, 1990). In addition, new statistical strategies that attempt to quantify the strength of spatial associations may allow us to strengthen inferences from spatial pattern analyses.

Over the last several years, methods based on Ripley's $L(t)$-function, and particularly Ripley's $L_{1,2}(t)$-function, have undergone rapid development and are now being widely used in plant ecology (Duncan, 1991; Haase et al., 1996; Barot et al., 1999; Goreaud et al., 1999; Mast and Veblen, 1999; Camarero et al., 2000; He and Duncan, 2000; Szwagrzyk et al., 2001; Call and Nilsen, 2003; Goreaud and Pélissier, 2003; Wiegand and Moloney, 2004). My argument in favor of Ripley's $L_{1,2}(t)$-function is that it uses the information from all inter-point distances between observed units, and therefore provides more information on the scale of the pattern than do statistics that use nearest neighbor distances only (i.e. Diggle's nearest neighbor functions G or F (Diggle, 1983; Barot et al., 1999)). Second, the function describes the characteristics of the point pattern over a range of distance scales, and can therefore detect mixed patterns (e.g. association at smaller distances and repulsion at larger distances). This is an important property because virtually all ecological processes are scale dependent and their characteristics may change across scales (Levin, 1992; Gustafson, 1998; Wiegand and Moloney, 2004). However, this qualitative determination of association or disassociation based on significance testing makes it difficult to *quantitatively* compare different cases, and further to evaluate hypotheses regarding the underlying processes involved. I propose the use of an index of association based on the relative strength of positive or negative association present in a particular bivariate point pattern at a particular distance.

Under the assumption that processes generate patterns, I tested links between patterns of spatial association among saplings and overstory trees and relative moisture availability in managed uneven-aged ponderosa pine/Douglas-fir forest stands in western Montana. I examined the spatial pattern of overstory and understory trees on stem-mapped plots in these managed stands. The $L(t)$-function (Besag, 1977), a transformation of the original Ripley's $K(t)$-function (Ripley, 1977), was used to evaluate the univariate spatial pattern of individual species and size classes (i.e., clumped, uniform, or random), while the intertype function $L_{1.2}(t)$ (Lotwick and Silverman, 1982; Diggle, 1983) was used to evaluate bivariate spatial association between species and size classes. Statistics summarizing of univariate and bivariate spatial patterns were evaluated to test the following hypotheses: 1) the spatial distributions of young cohorts of ponderosa pine and Douglas-fir in the understory are clumped; 2) saplings of ponderosa pine and Douglas-fir are negatively associated with each other (i.e., the two species are utilizing different microsites or one species might be excluding the other); and 3) the saplings of these species are negatively associated with older cohorts (i.e., positively associated with canopy openings). In addition, I utilized a novel strategy to numerically measure the strength of spatial association between tree size-classes in order to evaluate potential causal factors for such associations. I used this "index of association" to examine whether some of the variation in the degree of spatial association (or disassociation) between saplings and overstory trees could be explained by minor differences in relative moisture availability among our study sites.

3.2 METHODS

3.2.1 Study area

The study area was located in western Montana, approximately 170-km northwest of Missoula, on the Flathead Indian Reservation (FIR) of the Salish and Kootenai Tribes (Sanders County). The mean annual precipitation in the lower elevation forests examined for this study is between 400-520 mm (1999). The soils are formed from residual and colluvial materials eroded from Precambrian metasedimentary rocks (Belt formations), as well as unconsolidated tills deposited by glaciers. Ponderosa pine and Douglas-fir are the dominant tree species in the study area, along with scattered western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Dougl. ex. Loud). The natural disturbance regime in these forests had historically been dominated by low-severity ground fires with a return interval of 5-30 years (Habeck and Mutch, 1973; Arno, 1980; Fisher and Bradley, 1987; Arno et al., 1995b).

There is a longer history of uneven-aged management using single-tree selection on the Flathead Indian Reservation (FIR) than for most ownerships in Western Montana. Stands selected for this study on the FIR represented typical uneven-aged management regimes currently being recommended and implemented for ponderosa pine forests in the Northern Rockies region (Fiedler et al., 1988; Becker, 1995). Over the past forty years, the current study stands have been managed by some form of selective harvesting on a cutting cycle of ~20–25 years. The most recent harvest entry in study stands occurred between 14-18 years ago (1987-1991). Guidelines for individual tree selection system targeted a relatively low post-harvest basal area of 11-13 m^2/ha across stands, to be distributed among three to five age classes. However, basal area stocking levels sampled within ten 0.1 ha study plots approximately fifteen years after selection harvest ranged between 12.2 – 39.1 m^2/ha (Table 3.1).

Table 3-1. Stand structural characteristics for the 10 sampled stands on the Flathead Indian Reservation, Western Montana, sampled in 2002.

	Basal Area (m^2/ha)				Density large trees (#/ha) ¶				Density saplings (trees/ha)			
Plot	PP§	DF	WL	Total	PP	DF	WL	Total	PP	DF	WL	Total
1	13.1	4.7	0.0	17.8	100	155	0	255	532	3222	0	3754
2	17.5	6.5	0.0	24.0	146	119	0	265	202	440	0	642
3	3.6	10.0	6.9	20.5	18	229	91	338	73	2387	64	2524
4	24.9	0.0	0.0	24.9	881	0	0	881	624	0	0	624
5	10.1	2.1	0.0	12.2	294	36	0	330	367	54	0	421
6	16.0	1.5	0.0	17.5	247	54	0	301	1257	367	9	1633
7	8.2	16.9	0.2	25.3	82	321	9	413	192	1055	9	1256
8	9.1	18.5	0.0	27.6	431	431	0	862	275	238	0	513
9	37.0	2.1	0.0	39.1	358	91	0	459	725	1836	0	2561
10	22.9	1.8	0.0	24.7	440	100	0	540	2488	1286	0	3774

¶ Large overstory trees represent trees with a DBH larger than 30-cm; Saplings represent small trees with a DBH smaller than 5-cm and a height larger than 0.5-m

§ PP = ponderosa pine (*Pinus ponderosa*); DF = Douglas-fir (*Pseudotsuga menziesii*); WL = Western larch (*Larix occidentalis*).

3.2.2 Field sampling

In each of the ten study stands, I randomly established one 33 x 33 m square plot (~0.11 hectare), allowing that locations including the presence of perennial streams, rock outcrops, roads, or log yarding areas within plot boundaries were to be relocated. The azimuth and distance (to nearest mm) from the plot center to the center of each tree > 0.5 m tall was estimated using a handheld laser range finder (Forest Pro, Laser Technology, Colo., USA) and a compass. These field measurements were later converted to Cartesian coordinates using trigonometric functions. For each mapped tree, I recorded the species and measured diameter at breast height (DBH, 1.37 m) for classification into different size classes used in the spatial pattern analyses. Understory trees taller than 0.5 m but less than 5 cm DBH were classified as saplings, while those with bole diameters between 5-15 cm DBH were classified as small poles. Trees in the size range of 15-30 cm DBH were referred to as medium overstory trees, and all individuals exceeding 30 cm DBH as large overstory trees. In order to avoid overlap between size classes in the bivariate analysis of spatial pattern, I excluded the small pole size class from the analyses and instead focused on the relationship between saplings to medium and large overstory trees.

3.2.3 Habitat type designation

All of the stands sampled in this study are located on low to moderate productivity sites within a relatively narrow range of habitat types (Pfister et al., 1977) in the Douglas-fir series (i.e., they support Douglas-fir as the late-successional dominant in the absence of disturbance). There are slight differences in moisture availability across the sites, however, which are reflected in the floristic composition, including whether or not they will support western larch. In order to evaluate the effect of relative moisture availability on bivariate spatial patterns among saplings and overstory trees with our index of association strength, I used the Pfister et al. (1977) floristic habitat type classification system as a surrogate for site moisture level and stratified the ten sites into three habitat type groups. Such grouping of assemblages of habitat types with similar environmental regimes, responses to disturbance, and potential species composition and stand structure have been widely used in Western Montana as a coarse filter for ecological delineation of different vegetation response units in a management area (Chew et al., 2004). The three habitat type groups for this analyses are referred to simply as dry, moderate, and moist, though it is recognized that these are relative terms and that most all sites at this elevation in Western Montana experience some level of moisture stress during the growing season of most years.

3.2.4 Spatial pattern analysis

To simplify stand spatial structure, I focused on the two-dimensional location of stems in the stand. Therefore, the sampled area is represented by the horizontal plane bounded by plot borders, and each tree is represented by a point, defined by coordinates (x,y). The stem-mapped plot is thus reduced to a finite set of points, called a point process, the properties of which describe the horizontal spatial structure of the forest stand for each species and tree size class. Two types of null hypotheses concerning the type and intensity of the spatial distribution of tree stems were assessed using univariate and bivariate Ripley's *K*-functions and the related *L*-function (Besag, 1977; Ripley, 1981). The first null hypothesis for univariate spatial analysis is that there is no deviation from a distribution of complete spatial randomness (CSR). The second null hypothesis for bivariate spatial analysis is that the distribution of size-class of trees (or species) is independent of other size-classes (or species) in the sampled community (Goreaud and Pélissier, 2003).

The Ripley's *K*-function is defined so that $\lambda * K(t)$ is the expected number of neighbors in a circle of radius t centered at an arbitrary point of the pattern (Ripley, 1977), under the assumptions of stationarity (invariance of the process under translation) and isotropy (invariance of the process under rotation) (Haase, 1995; Dale, 1999; Goreaud et al., 1999). To simplify interpretation, it has become popular to use a linearized version of K(t): $L(t) = \sqrt{(K(t)/\pi)} - t$ proposed by Besag (1977) and estimated as:

$\hat{L}(t) = \sqrt{(\hat{K}(t)/\pi)} - t$, where $\hat{K}(t)$ is the estimated Ripley's K-function. This transformation makes $K(t)$ approximately linear in t, and scales its variance to facilitate comparison against the null hypothesis of complete spatial randomness (CSR) (Skarpe, 1991). The linearized function has an expectation of zero for any value of t when the pattern is random. The statistical significance of the departure from zero was tested using a Monte Carlo procedure that randomly repositions all points in the plot and generates $L(t)$ functions (Upton and Fingleton, 1985). In this study, I computed 99% confidence bands for $L(t)$ by running 99 simulations at intervals of 1 m from 1 to 16 m (half the length of the shortest side of the plot). The Cramer-von Mises test was used to test for significance (Haase, 2002). Since edge effects become a concern at greater distances, I used the weighted edge correction factor proposed by Ripley (1981) to account for this effect (Haase, 1995). If the deviation of the sample statistic, $\hat{L}(t)$, from zero expectation (CSR) is significantly positive or negative, a clumped or over-dispersed distribution of the sampled trees can be asserted, respectively (Diggle, 1983; Haase et al., 1996).

To test the second null hypothesis, that of spatial independence between different species or size-classes of trees, I used the modified $L_{1.2}(t)$-function (Lotwick and Silverman, 1982; Diggle, 1983). The classical estimator for this function is $\hat{L}_{1.2}(t) = \sqrt{(\hat{K}_{1.2}(t)/\pi)} - t$, where $\hat{K}_{1.2}(t)$ is the standard estimator of the intertype Ripley's K-function $K_{1.2}(t)$ proposed by Lotwick and Silverman (1982). Of particular interest was to examine whether the spatial distribution of saplings was independent of overstory trees. For this I assumed that the spatial patterns of the two different size-classes (or species for similar tests) were generated by two independent processes (e.g., different dispersion process periods, different species); hence, the null model of independence was adopted (Dixon, 2002; Goreaud and Pélissier, 2003; Wiegand and Moloney, 2004). The $\hat{L}_{1.2}(t)$ function quantifies the degree and type of spatial association between size-class (or species) 1 and 2. If the value of $\hat{L}_{1.2}(t)$ is not significantly different from zero, the null hypothesis that the two species have independent spatial distributions cannot be rejected (Kenkel, 1988; Goreaud and Pélissier, 2003). A value of $\hat{L}_{1.2}(t)$ significantly larger or smaller than 0 indicates spatial attraction or repulsion, respectively, between the two size-classes at range t. Monte Carlo simulations were used to evaluate the statistical evidence of a departure from zero, where each simulation consisted of randomly assigning new coordinates to only one size-class, while the coordinates of the other size-class remain unchanged (Haase, 2002; Goreaud and Pélissier, 2003). The spatial statistics program SPPA.EXE (Haase, 2002) was used for the computations of both univariate and bivariate analyses.

3.2.5 Strength of association

In the case of the bivariate Ripley's $L_{1.2}(t)$-function, the null hypothesis being tested was that there was no spatial association between two size-classes of trees. If the value of $\hat{L}_{1.2}(t)$ deviates significantly from 0, up to a distance t, this indicated spatial attraction or repulsion between the two size-classes up to that distance t. From this analysis we could answer preliminary questions about the observed patterns, such as whether the saplings had a negative spatial association with overstory trees, but we could not compare different plots. My approach to quantifying the relative strength of positive and negative associations is rather intuitive, in that it considers the ratio between the value of $\hat{L}_{1.2}(t)$ and the corresponding (upper or lower) confidence envelope (CE) at a specific distance t

(IA (t) = $\hat{L}_{1,2}(t)$/CE; Fig. 1). For a particular distance t, larger index values (in absolute value) indicate greater departures from the independence hypothesis. This index of association (IA) might logically represent the numerical strength of the point process up to a distance t (given the cumulative nature of the original function), and becomes useful when comparing groups of plots belonging to different ecological site types (e.g., habitat type groups). When comparing means, I aggregated plots to three different habitat type groups as described above to characterize minor differences in moisture availability (labeled dry, moderate, and moist) and assigned an IA value to each plot for distances t = 5 m and t = 10 m. These distances were selected assuming that 5-m was a fair representation of crown extension, and that 10 m extended far beyond crown influence (though perhaps not beyond the influence zone of roots). This allowed me to test the hypothesis that the strength of spatial association between saplings and overstory trees (medium and large) was not related to the habitat type group (i.e., moisture availability) of the site. Comparisons of IA for individual associations (i.e., ponderosa pine saplings vs. large trees) among different habitat type groups (moisture levels) were conducted using one-way ANOVA. These analyses were carried out with SPSS (2000).

3.3 RESULTS

3.3.1 Spatial distribution of natural regeneration

The mean density of naturally regenerated saplings (> 0.5 m tall, < 5 cm DBH) on the ten study stands was 1775 trees/ha (range of 421 – 3774), with approximately 31% ponderosa pine and 68% Douglas-fir (Table 3.1). Saplings of both species exhibited clumped distributions in the understory of these managed uneven-aged stands. Ponderosa pine saplings appeared clumped in all ten plots. For the nine plots where at least 20 saplings were present, this clumped pattern was significant across all distance classes (t) between 1 and 12-m (Table 3.2). Douglas-fir saplings were similarly consistent in displaying a clumped distribution across the range of distances examined (Table 3.2). For eight of ten plots with at least 20 Douglas-fir saplings present, all were significantly clumped, and seven plots exhibited this clumped pattern for all distances up to at least 9-m.

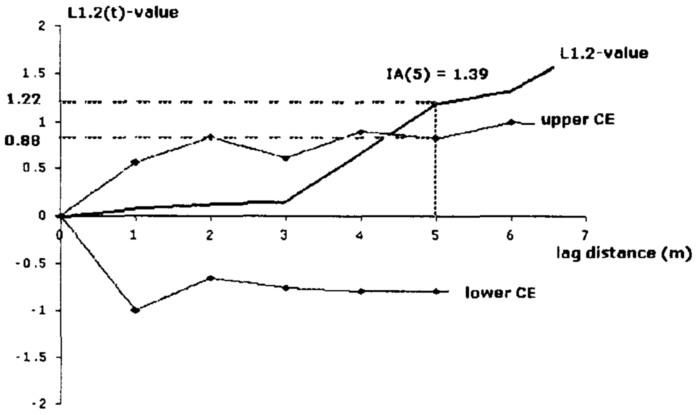


Figure 3-1. Index of association (IA) as a relative measure of the strength of association between two classes of points based upon the bivariate $\hat{L}_{1.2}(t)$ function and the confidence envelopes (CE) associated with it. The IA is the ratio of the $\hat{L}_{1.2}(t)$ value to the corresponding confidence band for a specific lag distance *t* (i.e., upper confidence band in the case shown).

There was no evidence in the data to support the bivariate hypothesis that saplings of ponderosa pine and Douglas-fir were negatively associated. A negative spatial association was not found in any plot at any scale. Instead, I found a positive spatial association for saplings of these two species in all but one of the plots where both were present (Table 3.2). In five of the seven plots where at least 20 saplings of each species were present, a significant positive spatial association was found at both small scales (up to 5-m) and at larger scales (10-m or greater).

Table 3-2. Patterns of spatial dispersion and association for saplings (taller than 0.5-m and less than 5-cm DBH) in 10 stands of ponderosa pine and Douglas-fir in Western Montana. Data for each stand are from a 33 x 33 m stem-mapped plot.

Plot		Ponderosa pine saplings																		Douglas-fir saplings																
		Distance t (m) *																		Distance t (m)																
	n§	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	p¶	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	p
1	58	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	351	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
2	22	c	c	c	c	c	c	c	c	c	c	c	c					0.01	48	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
3	8	c	c	c	c	c												0.10	260	c	c	c	c	c	c	c	c	c								0.01
4	68	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	0																	------
5	40	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	6																	0.76
6	137	c	c	c	c	c	c	c	c	c	c	c	c					0.01	40			c	c	c	c											0.01
7	21	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	118	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
8	30	c	c	c	c	c	c	c	c	c	c	c						0.01	26	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c		0.01
9	79	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01	201	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	0.01
10	140	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c		0.01	271	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c		0.01

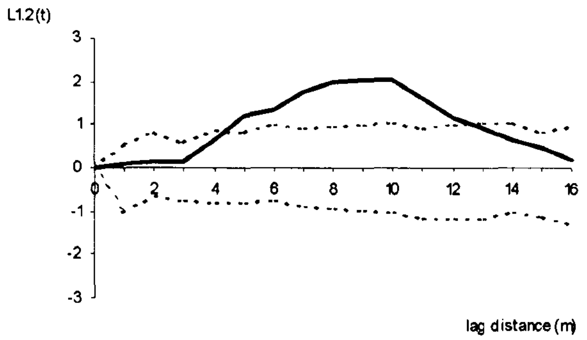
		Ponderosa pine vs. Douglas-fir saplings	
		Distance t (m)	
	N1/n2	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16	p
1	58/351	+ + ++ + ++ + ++ + + + +	.01
2	22/48	+ + + + + + + +	.01
3	8/260	+ + + +	.03
4	68/0		---
5	40/6	+ + + + +	.01
6	137/40	+ + ++ + ++ + ++ + + + +	.02
7	21/118	+ + ++ + ++ + ++ + + + + +	.01
8	30/26	+ + ++ + ++ + ++ + + + + +	.01
9	79/201	+ + ++ + ++ + ++ + + + + + ++	.01
10	140/271	+ + +	.08

§ n represents the number of individuals in the plot subjected to analysis; n_1 stands for the number of individuals in the plot belonging to the first size-class under analysis; n_2 corresponds to the second size-class

* The symbol *c* indicates a significantly clumped distribution; *u* indicates a regular distribution at distance *t*, based on the distribution of $L(t)$-function values. No symbol indicates a random distribution. The symbol + indicates significant positive association between both species; - indicates significant negative association at distance t, based on $L_{1,2}(t)$-function. No symbol indicates independence.

¶ Significance is evaluated using 99% Monte Carlo confidence intervals (99 simulations) with a 1-m step. The Cramer-von-Mises test was used to test for overall significance of patterns over the complete range of t, with p-values reported in the column titled "p".

a) Medium overstory trees vs. PP saplings up to 5-m



b) Medium overstory trees vs. DF saplings up to 5-m

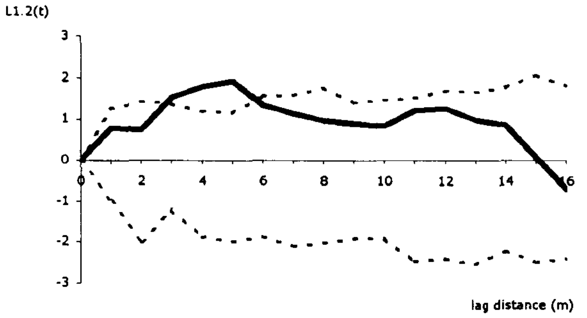


Figure 3-2. $\hat{L}_{1.2}(t)$ function and the confidence envelopes (CE) associated with it for the spatial association between medium-sized overstory trees (15-30-cm DBH) and (a) ponderosa pine saplings and (b) Douglas-fir saplings in plot 6. The association between the two size-classes in this example tends to be positive (attraction).

3.3.2 Association of saplings with overstory trees

In these managed multi-aged stands, the pattern of bivariate spatial association between saplings of ponderosa pine and Douglas-fir and overstory trees depended upon the level of discrimination among different overstory size classes. When the ponderosa pine saplings (< 5-cm DBH) were compared against the medium-sized overstory trees (15-30-cm DBH), two plots exhibited a significant positive spatial association at scales less than

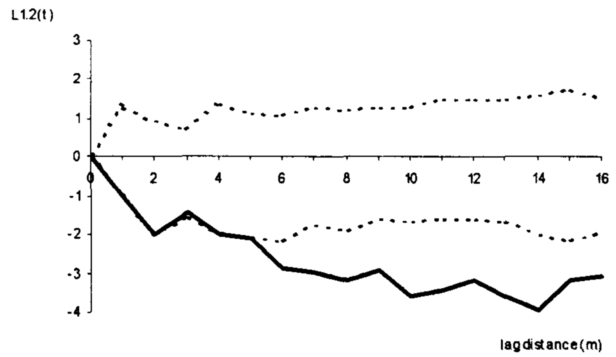
10 m (Figure 3.2a), while two other plots had a significant negative spatial association at the same scales (Figure 3.3a). In the other six plots there was no particular association evident. Similarly, there was no consistent trend in bivariate association between ponderosa pine saplings and large overstory trees (>30-cm DBH). While five of the ten plots exhibited a significant negative association between pine saplings and large overstory trees at larger scales, two plots displayed a positive association for comparable distances between 6 to 11-m (Table 3.3).

Mixed results were also observed for the bivariate association between Douglas-fir saplings and medium and large overstory trees. For the nine plots in which Douglas-fir saplings were present, they were negatively associated with medium sized trees in four plots (Figure 3.3b) and positively associated in three other plots (Figure 3.2b). Spatial association of Douglas-fir saplings with large overstory trees was likewise mixed, though a greater proportion of plots exhibited a negative association. I found a significant negative association between Douglas-fir saplings and large trees in four plots, whereas two plots had a positive association (Table 3.3).

3.3.3 Sapling-overstory associations in relation to habitat type groups

The analysis of variation in the "index of association" (IA) among different habitat type groups indicated that some of the above variation in the spatial association between saplings and overstory trees could be related to site differences in moisture availability (Table 3.4). Particularly for the association between saplings and medium sized overstory trees at short scales (up to 5-m); there appeared to be a shift from positive association on drier sites to a negative association on somewhat moister sites. For Douglas-fir, this same relationship was found to be significant in the ANOVA showing clear differences between the dry and moist habitat type groups (Table 3.5; Figure 3.4b). For Ponderosa pine, the same trends were evident, but were not significant (p-value=0.06) (Table 3.5; Figure 3.4a). A similar shift in the association between saplings and medium size overstory trees from positive on drier sites to negative on more moist sites was evident at the 10-m distance as well for both species, but the ANOVA results were not statistically significant (Table 3.5; Figure 3.5). For bivariate associations between saplings and large overstory trees, there were no significant differences among the different habitat type groups (*results not shown*).

a) Medium overstory trees vs. PP saplings up to 5-m



b) Medium overstory trees vs. DF saplings up to 5-m

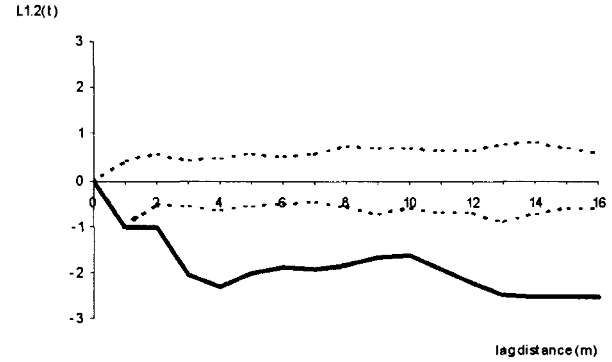


Figure 3-3. $\hat{L}_{1.2}(t)$ function and the confidence envelopes (CE) associated with it for the spatial association between medium-sized overstory trees (15-30-cm dbh) and (a) ponderosa pine saplings and (b) Douglas-fir saplings in plot 7. The association between the two size-classes in this example tends to be negative (repulsion).

Table 3-3. Patterns of spatial association for sapling size trees and both medium (15-30 cm DBH) and large (> 30 cm DBH) overstory trees, by species within stem mapped plots of ten managed, uneven-aged ponderosa pine/Douglas-fir stands in Western Montana.

Plot		Ponderosa pine saplings vs. medium overstory trees																
		Distance t (m) *																
	n1/n2§	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	p¶
4	68/32																	.41
5	40/13	+	+	+	+	+	+	+	+	+	+	+	*					.01
10	140/9																	.12
1	58/11																	.06
2	22/7																	.88
6	137/9					+	+	+	+	+	+	+	+					.01
8	30/25						+	+										.11
3	8/14																	.42
7	21/16				-	-	-	-	-	-	-	-	-	-	-	-	-	.01
9	79/20			-	-	-	-	-	-							+	+	.01

Plot		Douglas-fir saplings vs. medium overstory trees																
		Distance t (m)																
	n1/n2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	p
4	0/32																	----
5	6/13					+	+	+	+	+								.05
10	271/9																	.86
1	351/11					+	+	+	+	+	+	+	+	+	+	+	+	.01
2	48/7										-	-	-	-	-			.01
6	40/9			+	+	+												.12
8	26/25	+							+	+	+	+						.08
3	260/14			-	-	-	-	-					-					.01
7	118/16		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01
9	201/20				-	-	-	-	-	-	-							.01

		Ponderosa pine saplings vs. large overstory trees																
		Distance t (m) *																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
4	68/10				+	+				-	-							.03
5	40/7								+	+	+	+						.01
10	140/13							-	-									.12
1	58/7						+	+	+	+	+	+	+	+	+	+	+	.01
2	22/12											-	-	-	-			.03
6	137/6							-	-	-	-	-	-	-	-	-	-	.01
8	30/8				-	-	-	-	-	-	-	-	-	-	-	-	-	.01
3	8/9												-	-	-	-		.05
7	21/13														-	-	-	.06
9	79/19		-	-	-	-												.01

		Douglas-fir saplings vs. large overstory trees																
		Distance t (m)																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
4	0/10																	----
5	6/7															+		.18
10	271/13		-	-	-	-	-	-	-	-	-	-	-	-				.01
1	351/7						-									+	+	.20
2	22/12		+	+	+	+	+	+										.01
6	40/6									-								.13
8	26/8				-	-	-	-	-	-	-	-	-	-	-	-	-	.01
3	260/9												-	-				.01
7	118/13		-	-	-	-	-	-	-	-			-					.01
9	201/19								+	+	+	+	+	+	+	+	+	.01

§ n_1 stands for the number of individuals in the plot belonging to the first size-class under analysis; n_2 corresponds to the second size-class.

* The symbol + indicates significant positive association; - indicates significant negative association at distance t, based on $L_{1.2}(t)$-function. No symbol indicates independence.

¶ Significance is evaluated using 99% Monte Carlo confidence intervals (99 simulations) with a 1-m step. The Cramer-von-Mises test was used to test for overall significance of patterns over the complete range of t, with p-values reported in the column titled "p".

Plots 4, 5 and 10 are classified as drier; plots 1, 2, 6 and 8 are classified as moderate; and plots 3, 7 and 9 are classified as wetter.

3.4 DISCUSSION

Spatial pattern analysis of regeneration in ten managed uneven-aged stands selected for this study indicated that saplings of both ponderosa pine and Douglas-fir tend to be spatially clumped, though such aggregations are not necessarily associated with canopy openings. This finding of clumped regeneration patterns is similar to results reported for ponderosa pine occurring as even-aged patches in natural stands (Cooper, 1961; Mast and Veblen, 1999; Woodall, 2000). Each harvest in stands managed by single-tree selection may open up over 25% of the canopy area, and there is the potential for a fairly dispersed pattern of regeneration across the stand (Nyland, 2002). However, aggregated regeneration patterns in managed stands are likely driven by many of the same factors as found under natural stand dynamics. Various processes can lead to clumped patterns of recruitment, e.g., natural or mechanical soil disturbances creating patches of favorable seedbed, or increased resource availability within patches, as might be associated with canopy gaps (Veblen, 1992; Franklin et al., 2002). Clumped distributions of regeneration have likewise been reported in managed stands of *Picea abies*, *Abies alba*, and *Fagus sylvatica* (Fröhlich and Quednau, 1995) and in *Ailanthus altissima* and *Robinia pseudoacacia* (Call and Nilsen, 2003).

I found little evidence to suggest that saplings of ponderosa pine and Douglas-fir occupy separate spatial locations in these stands. The bivariate analyses for sapling distributions showed a general *positive* spatial association between these two species. Szwagrzyk (1992) reported a similar positive association between recruitment of two sympatric species, *Pinus sylvestris* and *Fagus sylvatica*. The existence of positive interactions between species has been reported to be common in many environments (Callaway, 1995; Holmgren et al., 1997). However, these positive associations have generally been reported for different layers or life forms (e.g., seedlings of one tree species and adults of another shrub species -Callaway (1992)) rather than species belonging to the same life form (e.g., trees only).

Table 3-4. Index of association (IA) values from the $\hat{L}_{1.2}(t)$ function up to 5 and 10-m (short and larger scale, respectively) for the spatial association between saplings and overstory trees in 10 plots (33x33-m) of ponderosa pine and Douglas-fir in Western Montana.

		5-m				10-m				5-m	10-m
		PP§		DF		PP		DF		PP vs. DF	PP vs. DF
Habitat Type	Plot	Medium ¶	Large	Medium	Large	Medium	Large	Medium	Large		
Dry	4	-.109	-1.145			-.268	1.134				
Dry	5	.1656	-.257	1.216	-.185	1.081	1.541	-1.245	.142	1.157	.921
Dry	10	.772	-.777	.387	-1.528	.781	-.632	.922	-2.270	.530	.331
Moderate	1	.228	.070	.445	-.505	.246	1.072	3.110	.205	2.760	1.979
Moderate	2	.010	.462	-.309	1.331	-.165	-.878	-1.251	-.848	1.351	.714
Moderate	6	1.455	-.746	1.648	-.264	1.950	-1.506	.574	-1.111	1.845	1.071
Moderate	8	.309	-2.321	.687	-1.508	.782	-1.897	1.091	-1.585	3.093	1.941
Moist	3	-.019	-.202	-1.079	-.192	.082	-.302	.723	-.222	-.166	-.304
Moist	7	-1.029	-.340	-3.743	-5.353	-2.204	-.419	-2.750	-.788	2.319	1.757
Moist	9	-2.054	-1.960	-1.199	.579	-.348	-.044	-1.202	1.320	4.115	3.094

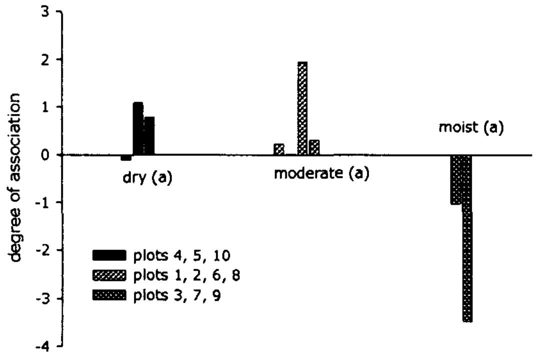
§ For saplings only: PP = ponderosa pine (*Pinus ponderosa*); DF = Douglas-fir (*Pseudotsuga menziesii*); WL = Western larch (*Larix occidentalis*)

¶ Large overstory trees represent trees with a DBH larger than 30-cm; Medium overstory trees are trees with a DBH between 15-30-cm; Saplings represent small trees with a DBH smaller than 5-cm and a height larger than 0.5-m.

Whereas the spatial association of ponderosa pine and Douglas-fir would be easily explained if they were found to occur together in canopy gaps, I did not find that saplings were consistently clumped and separated from overstory trees (i.e., in gaps). In general, ponderosa pine and Douglas-fir saplings were either positively associated with medium-sized overstory trees (15-30 cm DBH) or independently distributed in more than half of the sample plots. In moisture-limited sites, like those examined in this study (400-520 mm/year), we might expect to see a reduced spatial association between regeneration and canopy gaps. In such sites, canopy openings are potentially less hospitable to new germinants susceptible to excessive surface temperatures and moisture stress. Germinants may recruit throughout the stand wherever available seed falls on suitable seedbeds, but survival on dry sites may be favored by the shade provided by close proximity to overstory trees. It has been argued that on more xeric habitats, reduced moisture stress under adult tree canopies may explain the increased sapling abundance beneath their canopies (Niering et al., 1963; Callaway, 1992; Bertness and Callaway, 1994). This positive spatial association may result from a facilitative relationship of larger "nurse plants" providing shelter to seedlings by buffering physical stresses, especially high temperature. Bertness and Callaway (1994) suggested that facilitation can potentially play a more important role than competition in stressed and resource-limited environments. These findings support this explanation when considering medium-sized but not necessarily larger overstory trees (>30-cm DBH) (see below). However, a positive association between regeneration and adult trees might be expected to shift over time as greater resource requirements of larger regeneration leads to more direct competition with the overstory layer (Holmgren et al., 1997). While a positive association between regeneration and adult trees may be important for establishment at early development stages, once the new seedlings become established, they are likely to experience a more competitive relationship with overstory trees.

In order to further investigate bivariate associations in relation to slight differences in moisture availability between study sites, I introduced an intuitive approach to characterize the *strength* of association patterns that I termed the index of association (IA). This approach to quantifying the degree of spatial association can be used to examine the correlation between observed patterns and potential causal factors, thereby extending the utility of spatial pattern analysis. These analyses (ANOVA) relating the strength of spatial association to the three habitat type groups (i.e., moisture availability levels) indicated significant differences according to habitat type in the bivariate association between saplings and medium-sized overstory trees (15-30-cm DBH) at small scales. Saplings were positively associated with these medium-sized overstory trees in plots belonging to dry and moderately dry habitat type groups, while negatively associated in plots belonging to moist habitat types. When considering larger overstory trees (>30-cm DBH), there were no such differences between IA values for bivariate association of saplings and overstory trees among different habitat type groups for saplings when compared to overstory trees. Regarding "nurse plant" effects, I can speculate that on drier sites, saplings may experience reduced desiccation and higher survival rates when located in close proximity to taller trees. However, this "nurse plant" effect was detected for spatial associations between saplings and medium-sized overstory trees only, and not when larger overstory trees (> 30-cm DBH) were compared. Two explanations can be proposed for this difference between overstory size classes. First, the positive association for saplings and medium-sized overstory trees could be related to a common dispersal process; such that saplings are later arriving recruits (or similar aged, but suppressed individuals) from the same regeneration event as larger pole sized trees and therefore continue to be spatially associated. But having anticipated the potential confounding effect of such an overlap in adjacent size classes, I had decided to avoid bivariate analysis of saplings (< 5-cm DBH) with small poles (5-15-cm DBH), and instead to examine only associations with overstory tree size classes > 15-cm DBH. A second explanation for the difference between overstory size classes would be that medium-sized trees may be effectively providing more shelter to saplings than large overstory trees due to their having lower crown heights. It is possible that the ameliorating effect of larger "nurse trees" on temperature and moisture stress could be more pronounced for trees having the base of their live crown in closer proximity to the regeneration, such that the shade cast over young recruits is effective at short distances (i.e., smaller 5-m scale in our spatial analyses).

(a) Medium overstory trees vs. PP saplings up to 5-m



(b) Medium overstory trees vs. DF saplings up to 5-m

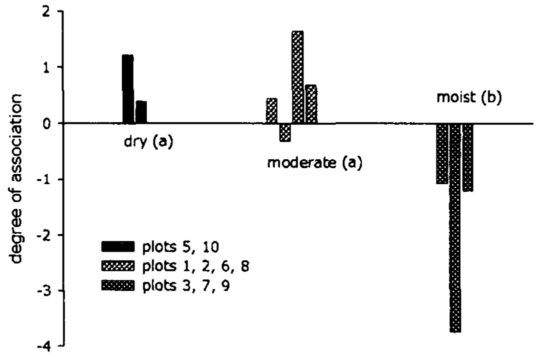


Figure 3-4. Index of association (IA) among the three habitat-type groups at 5-m lag distance for the spatial association between medium overstory trees (DBH between 15-30-cm) vs. (a) ponderosa pine (PP) and (b) Douglas-fir (DF) saplings. Letters in brackets, when different, indicate significant differences between habitat type groups (p=0.05).

The results of this study have some interesting silvicultural implications for the establishment and release of regeneration in ponderosa pine/Douglas-fir forests managed under the individual tree selection system. While I found seedlings of both ponderosa pine and Douglas-fir tended to be clustered in patches, their establishment did not appear to be closely associated with locations under canopy gaps. It is one of the tenets of uneven-aged management under the selection system that recruitment of new age classes should be secured at each cutting as growing space is freed up by the harvested trees (Smith et al., 1997; Nyland, 2002). The available growing space is often conceptualized as being primarily within canopy openings (and associated root gaps) created by the removal of one or more mature trees, particularly when considering shade intolerant species that may require large gaps for successful recruitment into the overstory (Runkle, 1982; Canham and Marks, 1985; McClure and Lee, 1993). However, under the low reserve stocking levels typical of individual tree selection guidelines for various intolerant pine species (Fiedler et al., 1988; Baker et al., 1996; Shelton and Cain, 2000; Palik et al., 2002), initial establishment of regeneration is often more diffuse across the stand. In western Montana, reserve basal area stocking levels for uneven-aged management of ponderosa pine are typically targeted between 9-13 $m^2\ ha^{-1}$, a level which local permanent plot data suggest will capture the site's growth potential while allowing for consistent regeneration of seral pine and larch (Fiedler et al., 1988; Becker, 1995). The current analysis suggested that the regeneration established under this management regime was no more likely to be found under canopy gaps than in association with overstory trees, particularly on drier sites. Given this potential for diffuse distribution, managers should plan for any site preparation treatments promoting natural regeneration (e.g., mechanical or prescribed fire) to be conducted throughout the stand, rather than limiting their focus to canopy openings. Moreover, since the number of sapling recruits needed at each cutting cycle is relatively small (<100 ha^{-1}), securing broad distribution (i.e., full stocking) of desirable regeneration may be more important than the absolute density of saplings established (Becker, 1995).

Table 3-5. F-values and probability values from the one-way ANOVA between the index of association (IA) and the habitat type groups. The IA values are from the $\hat{L}_{1.2(t)}$ function up to 5 and 10-m (short and larger scale, respectively) for the spatial association between saplings and overstory trees in 10 plots (33x33-m) of ponderosa pine and Douglas-fir in Western Montana.

Distance	5-m				10-m				5-m	10-m
Species	PP §		DF		PP		DF		PP vs. DF	PP vs. DF
Overstory tree size-class	Medium ¶	Large	Medium	Large	Medium	Large	Medium	Large		
F-value	4.189	0.035	6.361	0.400	2.422	1.667	3.587	0.911	0.755	0.459
					P-values					
General *	0.064	0.966	0.033	0.687	0.159	0.256	0.094	0.451	0.510	0.652
Comparisons										
HT1 vs. HT2	0.682	0.906	0.849	0.742	0.822	0.111	0.962	0.815	0.279	0.432
HT1 vs. HT3	0.033	0.898	0.028	0.688	0.128	0.318	0.087	0.282	0.360	0.409
HT2 vs. HT3	0.047	0.799	0.018	0.405	0.076	0.523	0.047	0.299	0.875	0.919

§ For saplings only: PP = ponderosa pine (*Pinus ponderosa*); DF = Douglas-fir (*Pseudotsuga menziesii*); WL = Western larch (*Larix occidentalis*)

¶ Large overstory trees represent trees with a DBH larger than 30-cm; medium overstory trees are trees with a DBH between 15-30-cm; saplings represent small trees with a DBH smaller than 5-cm and a height larger than 0.5-m

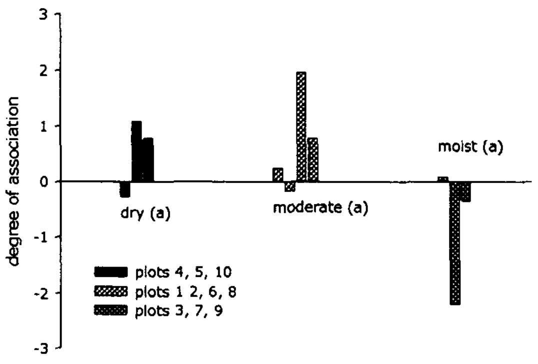
* HT1: dry level habitat type group; HT2: moderate moisture level habitat type group; HT3: moist level habitat type group.

Whereas our analysis of the distribution of sapling occurrence indicates that establishment may not be tied to canopy gaps, such openings are very likely important for the release of saplings once established. The microsite conditions that are suitable for initial establishment clearly differ from optimal conditions for sustained sapling growth, in part because the shade tolerance of tree seedlings tends to decrease with increasing size

(Givnish, 1988; Messier et al., 1999). Any positive association we observed between young regeneration and adult trees would be expected to shift over time as the greater resource demands of larger saplings lead to more direct competition with the overstory layer (Holmgren et al., 1997). Subsequent selection harvests offer opportunities for releasing some of the saplings established in the previous cutting cycle. Given a diffuse distribution of regeneration across the stand, it may be more appropriate to consider canopy openings as areas where previously established saplings can be released, rather than as sites for establishing new regeneration. In locating new canopy openings, the presence of desirable saplings needing release would be taken into account along with which overstory trees might be selected for harvest.

One of the limitations of the current study is the focus on regeneration density within broad size classes. Regeneration in these analyses included saplings ranging from 0.5-m tall up to large saplings at 5-cm DBH. We might arrive at different conclusions about spatial association between regeneration and medium-sized and overstory trees if we look at very small first year germinants versus well-established advance regeneration. In addition, we did not evaluate the effects of overstory tree competition on the growth rates of regeneration, or the potential for faster growth rates in canopy gaps to lead more rapidly to reduced density of regeneration due to natural self-thinning. Further work is needed, beyond descriptions of spatial point patterns, to examine the effects of spatial patterns on individual tree-growth performances (i.e., mean annual increment, survival, and growth efficiency) as well as on stand-level growth given different growing space allocation among cohorts (Woodall, 2000).

(a) Medium overstory trees vs. PP saplings up to 10-cm



(b) Medium overstory trees vs. DF saplings up to 10-m

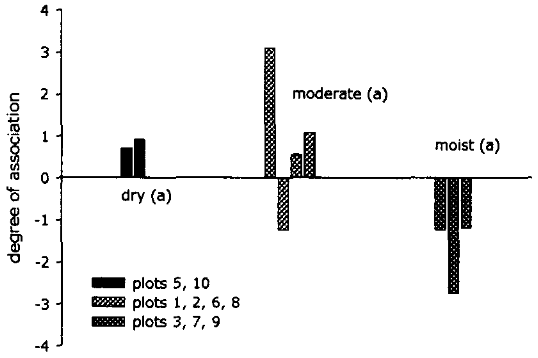


Figure 3-5. Index of association (IA) among the three habitat-type groups at 10-m lag distances for the spatial association between medium overstory trees (DBH between 15-30-cm) vs. (a) ponderosa pine (PP) and (b) Douglas-fir (DF) saplings. Letters in brackets, when different, indicate significant differences between habitat type groups (p=0.05).

3.4.1 Conclusions

Given that this is a descriptive study, we cannot draw definite conclusions about causal relationships for the observed patterns; many possible variables may affect plant-plant interactions and thus be responsible for the observed patterns discussed above (Bazzaz, 1990; Barot et al., 1999; Wyszomirski et al., 1999). However, if we ignore spatial interactions, we may risk being unable to accurately predict the dynamics of even a very simple ecological system, regardless of how accurately we measure the underlying demographic rates (Hastings, 1993). Strategies such as quantifying the strength of association may allow us to extend inferences from observed patterns of spatial associations. The index of association strength introduced in this paper should be assessed in other studies involving bivariate spatial pattern analyses. We expect that this or comparable indices could be useful for evaluating hypotheses regarding potential causes for observed spatial associations and thereby help to link functional and structural components of forest communities.

Chapter 4

DISTINGUSHING MICROSITE AND COMPETITION PROCESSES IN TREE STAND DEVELOPMENT: AN *A PRIORI* SPATIAL MODELING APPROACH

> "Competition arises from the reaction of one plant upon the physical factors about it and the effect of these modified factors upon its competitors. In the exact sense, two plants, no matter how close, do not compete with each other as long as the water content, the nutrient material, the light and heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plant, competition begins"(Clements et al., 1929).

> "Competition, which varies with tree size and stand density and directly influences tree vigor and growth, is very difficult to quantify."
>
> (Korol et al., 1995).

4.1 INTRODUCTION

One of the challenges of understanding plant population development is to determine the causes of size variation through time (Harper, 1977; Weiner, 1990; Pfister and Stevens, 2003). Variability in tree size reflects differences in the distribution of resources at a site (e.g., microsite variability) and the results of biological processes (e.g., competition) (Weiner, 1988). However the link between these factors affecting size and the observed patterns in the field is not fully understood. Size variability in plants is a consequence of first, a deterministic growth pattern that relates individual growth rate to current plant size, and second, stochastic growth patterns that represent variation in growth rates due to microsite heterogeneity, genetic variation and neighborhood effects (Hara, 1984; Bonan, 1988). These effects are normally confounded in long-lived species because experiments to distinguish these would require decades and for many questions may be impossible (e.g., manipulation of competition at age 10, independent of competition status at age 5 is not possible). In this study, I present a novel application of a standard spatial statistical tool to separate the confounded "stochastic" factors affecting forest stand development: microsite and competition. With these factors separated, I present an updated general model of forest stand dynamics.

In even-aged monospecific tree stands, at least two processes can be important in accounting for the observed spatial structure in tree size through time: competition and microsite variability. Competition, by definition, involves a struggle to pre-empt limiting resources such as light, water, and nutrients that, together, determine rates of carbon acquisition (Harper, 1977; Grime, 2001). Commonly, tree competition has been thought to be asymmetric: larger trees have a disproportionate competitive advantage (for their relative size) over smaller trees, suppressing their growth (Thomas and Weiner, 1989; Weiner, 1990; Schwinning and Weiner, 1998). If two trees are growing next to each other, competition will tend therefore to create a negative spatial autocorrelation in size among neighboring trees (Yoda et al., 1957; Bachacou and Decourt, 1976; Franco and Harper, 1988; Magnussen, 1994; Fox et al., 2001; Shi and Zhang, 2003). Microsite accounts for the heterogeneity in resource availability (e.g., soil type, moisture levels, nutrient availability) across a relatively small range that can alter the competition status among trees (Yastrebov, 1996; Wyszomirski et al., 1999; Bullock and Burkhart, 2005). However, microsite resource variation in space has mostly been assumed to be homogeneous when competition is analyzed (Gurevitch et al., 2002), or left as a stochastic process (Hara, 1984). The effect of microsite variation is often observed in young, pre-canopy closure stands and in older senescent stands (Bachacou and Decourt, 1976). Microsite processes will tend to create a positive spatial autocorrelation in size among neighboring trees; similar-sized trees surround other trees (Bachacou and Decourt, 1976; Bullock and Burkhart, 2005). The effect of microsite heterogeneity may also last longer in the development of the stand; however, it is believed that with time competition becomes more important at the population level, with trees suffering more from growing with large neighbors than they gain from being in a good patch (Stoll et al., 1994; Bullock and Burkhart, 2005).

These two processes, namely competition between trees and microsite effects, will create spatial structures in stand features, such as relative growth rate (RGR), that can be described by semivariograms. Theoretical semivariogram models (e.g., exponential, wave, spherical, etc.) can be fit to empirical semivariograms of RGR allowing the investigator to obtain parameters of the theoretical semivariogram and relate the observed structure to hypothesized generating processes (Bachacou and Decourt, 1976; Legendre, 1993; Kint et al., 2003). I propose that microsite processes usually differ in scale (range of semivariogram) and always in quality (shape of semivariogram) from competition interactions, and these differences in scale and quality can permit us to distinguish both processes. Therefore, we expect the spatial signatures of annual growth for the two processes to be different. In light of Chalmers's "sophisticated falsification" (Chalmers, 1999) I distinguish the two processes by making "bold" or precise conjectures. This conjecture states competition will create a spatial pattern best fit by a wave semivariogram: neighboring trees differ greatly in size and performance (Reed and Burkhart, 1985). Around a dominant tree there is usually a ring of suppressed trees. In turn, trees in the next concentric ring behave as dominants and so on (Law et al., 2001). The overall effect can be described by a density wave that damps down with distance, propagating in all directions from every tree. Furthermore, for a wave spatial structure to represent competition, the range parameter (see methods) must be at the spatial scale of the neighboring tree-tree distance (2-4m in our sites). A spatial pattern best fit by a wave semivariogram but with a range parameter greater than the nearest tree does not represent competition. Thus, in contrast to standard ecological model fitting where only the model form determines the model, here, both the model form and a strict range of parameter values represent the biological process of interest. In contrast to competition, microsite processes will be best fit by monotonic increasing semivariograms (exponential or spherical types). When large individuals have similar large neighbors, it is often considered evidence for homogeneous spatial resource availability (Figure 4.1).

Overall, this methodology of having the *spatial pattern* of a measurable variable (RGR) represent the value of an unmeasurable variable (competition or microsite effects) is called using space-as-a-surrogate (McIntire, 2004). It differs from a similar approach of examining the outcome of a process to infer characteristics of the process, known as inverse modeling, because I cannot directly measure the outcome of tree-tree competition. I can, however, quantify and analyze the *spatial pattern* of a measurable variable, and from this infer the process. This is an inference strategy that relies on linking biological mechanisms to spatial patterns, and is not simply an analysis tool.

Here, accepting that I can separate competition effects from microsite effects in developing forest stands, I introduce a generalized stand development model to include the influence of microsite and intraspecific interactions on growth. I considered 5 *a priori* hypotheses that tie directly to the two ecological processes that create the population structure (competition between trees and microsite effects) from soon after planting until 2004 (sampling year). Assuming that seedlings varied in size but, nonetheless, were planted at random, I expected that at early stages in stand development, RGR should show no spatial pattern (stochastic variation); it is too early for any spatial "manifestation" in plant RGR from specific differences in resource availability and competition (root or crown overlapping among trees is not probable). To the extent that the young stand develops prior to canopy closure, I expected that spatial differences in resource availability may appear, showing relatively "better" microsites, where trees share better growth rates and similarities in size (positive spatial autocorrelation). Once crown overlapping begins, I expected the onset of competition, which over time would express a short-scale size-hierarchy between neighbors with spatial discontinuity between such groups. After thinning is practiced (if any) and if it were randomly applied (which is not necessarily true), I would expect the model to start over again: no spatial pattern, site effect, and then competition.

In summary, I simultaneously tested three key elements: first, whether the proposed model of early stand development (i.e., initiation-no-interaction, microsite effect, followed by competition and (self) thinning) occurs, and whether it occurs similarly in all sites; second, how the timing and relative strength of microsite effects versus competition compare in early even-aged stands; and third, the application, evaluation and testing of a common geostatistical tool to disentangle these previously confounded processes. To evaluate the success of this approach, I used three separate assessments: first, the use of Ripley's K statistic to determine the presence and scale of microscale heterogeneity on the younger sites; second, whether I detect the typical stand development trajectory (initiation, growth, self thinning); and third, whether I avoid nonsensical results (such as high competition at time of planting, or random growth at time of self-thinning). I tested these elements in three ponderosa pine plantation stands of different ages, located in Patagonia, Chile.

4.2 METHODS

4.2.1 Study area and sampling

The plantation stands are located in the surroundings of Coyhaique city (lat. 45° 52' S and long. 72° 00' W; 900 m above sea level), Coyhaique province (Region XI), in the east-Andean foothills of Patagonia, Chile. This zone belongs to the supra-temperate belt with humid climatic conditions (Amigo and Ramírez, 1998). The annual precipitation falls mainly as snow, and is approximately 1100 mm in Coyhaique (Mirador and Cóndor stands), and 600 mm for Coyhaique Alto (Flamenco stand) (CONAMA, 1998). The soil is mainly derived from aeolian volcanic ash deposits. Ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) constitutes the most widely planted exotic species in the Patagonian Andes region of Chile and Argentina, where it grows vigorously and without any serious pest problems.

In January 2004, I randomly located two 0.17-0.35 ha plots within each of the three stands (Cóndor, Mirador and Flamenco), where ponderosa pine was the only species planted. The initial density of these plantations was 1666 trees per hectare (2 x 3-m arrangement). The three stands differed in plantation age, site quality and current density (more details in Table 4.1). In each plot I mapped and measured all trees. I estimated the coordinates of each tree stem center by using a hand-held laser range finder (Forest Pro, Laser Technology, Colo., USA) and a digital compass, which estimate the distance and azimuth to the center of each tree to the nearest 1-mm. The field measurements were converted to coordinates using trigonometric functions. For each mapped tree stem, I measured diameter at breast height (DBH; 1.35 m). For trees whose DBH was greater than 10 cm, I extracted one core to the pith at approximately 20-cm of height using an increment borer. When trees were larger than 20-cm DBH, I extracted two cores. Heights were measured with the laser range finder. I mapped, measured and cored a total of 1173 trees across the three stands. At the lab, I dried the tree cores, mounted them in grooved wooden boards, and sanded them with successively finer grades of sand paper to reveal annual rings. For each tree core, I measured radial annual width using a microscope mounted on a dendrochronometer with a Velmex slide. For cores that missed the pith of the tree, I followed procedures described by Duncan (1989) to estimate the number of missing rings. No correction was applied for time required to grow to coring height.

4.2.2 Relative growth rate

Analysis of growth rates for individual plants provides insights into the nature of size variation in even-aged monocultures. Since absolute growth is clearly a function of the initial size of a plant (Ford, 1984), growth rates are commonly expressed in relative terms. Relative growth rate (RGR) is usually the most appropriate measure of plant performance for use in a neighborhood analysis when plant size is incorporated into a measure of local interference. In particular, I used RGR because it does not necessarily minimize spatial dependencies among the data in the analysis (Stoll et al., 1994; Wagner and Radosevich, 1998), and because it is a measure of efficiency: an increment of unit of size per unit time (Gurevitch et al., 2002). Whatever the distribution of RGR, the mean RGR over an interval of 1-year is defined as:

$$RGR = (\ln BA_{t+1} - \ln BA_t) * 100$$

where BA_{t+1} is the basal area (in cm^2 at the base of the stem) at the end of the time interval (1 year) and BA_t is the BA at the start of the time interval (Hunt, 1990). Correspondingly, BAs were computed as:

$$BA_t = \pi * r_t^2$$

where r_t is the radius of the cross section at year t, based on the actual core length (from pith to annual ring). This simple BA computation is based on two assumptions relative to young pine tree plantations: first, the pith approximately represents the centroid of the cross section; and second, the stem cross-section is approximately circular. In regular spaced plantations, these assumptions are expected to be valid under most conditions.

4.2.3 Spatial autocorrelation and multiple hypothesis testing

Geostatistics is a collection of statistical methods for use in the presence of spatially autocorrelated data. Spatially autocorrelated data represent any variables that are distributed continuously in space, i.e., regionalized variables (Goovaerts, 1997; Wagner, 2004). Geostatistical analyses require response values that need to be labeled with the spatial coordinates at which measurements are collected. The basic principle of geostatistics is that correlation between values of a regionalized variable Z will decrease as distance between the sample points increases. I chose a geostatistical approach instead of using some standard competition index, because of the potential for geostatistical tools to better represent the link between spatial patterns and processes, by relying on the dependencies among observations. Competition indices based on regression analyses usually consider dependent observations, which violate standard statistical assumptions of independence of data points (Bullock and Burkhart, 2005): a tree may be a subject tree and a neighbor tree in the same regression analysis. A common alternative to this procedure is to use subject trees that are far apart; however, such methods ignore large amounts of data.

The variogram is the variance of the difference between random variables at two units (locations), given by: Var ($Z_i - Z_j$) for two sites i and j. The empirical semivariogram is one half the estimated variogram, and is defined as:

$$\hat{\gamma}(h) = 1/2 \cdot N(h) \cdot \sum_i [z(x_i) - z(x_i + h)]^2,$$

where: h is the distance lag between sampled trees, $N(h)$ is the number of paired comparisons at lag h, $z(x_i)$ and $z(x_i + h)$ are the observed tree variable values at location x_i and $x_i + h$, respectively (Webster and Oliver, 2001). Under a typical spatial dependence model, two units that are close together will have a smaller variance of the difference. As units get further apart, their differences get larger and usually the variance of the difference gets larger as well. The semivariogram is used to examine the degree of spatial continuity in data at various lags or distances of separation (Isaaks and Srivastava, 1989; Cressie, 1993). Nonetheless, wave semivariograms, as explored in this research, behave differently (see below).

Generally, single theoretical models are used for modeling empirical semivariograms that are close enough in shape to one of the basic admissible models, or for the approximate fitting of complex structural functions. In the case of spatial interpolation (e.g., kriging), the choice of the semivariogram model does not matter greatly as long as the model fits the data reasonably (Zimmerman and Harville, 1991; ver Hoef and Cressie, 2001). Here, however, I have two alternate ecological processes that will create different spatial signatures. To test this, I selected 5 different theoretical semivariogram models to analytically depict the spatial autocorrelation of RGR shown in the empirical semivariograms (Figure 4.1). In describing local microsite effects, I used two theoretical models that describe positive spatial autocorrelation continuity. These are the exponential and spherical models. I provide two different model forms for to represent microsite to allow for alternate shapes in the positive spatial autocorrelation. For competition among trees I used the "wave" model, which depicts a discontinuity in spatial autocorrelation at a short scale (neighboring trees differ greatly). The competition process is assumed to decay with distance so that the wave model captures the continued indirect effects of competition through many individuals. In addition, as described above, when fitting the wave variograms, I only accepted local optima for the range parameter that fall between 2 and 4-m, reflecting the inter-tree minimum distance. Note that it is not the wave theoretical variogram that *is* competition; it is a particular form of the wave function that represents competition. In many cases I can expect that both processes (competition and microsite) interact forming a complex structural function. For this, I built and tested a nested model that was a mixture between the wave and exponential model, and can detect competition occurring alongside microsite effects.

Finally, I also considered the "nugget" model (pure nugget effect) to test for a lack of spatial autocorrelation (stochastic variation). The nugget model suggests there is no spatial pattern or the scale at which the process is acting is smaller than the distance between two trees.

In a semivariogram, the estimated semivariance ($\hat{\gamma}$(h)) is plotted on the y-axis against lag distance (h) on the x-axis. The lag distance is the step-size used, and the active lag is the largest distance considered between points in the semivariance data set, though the whole data set is included in the analysis (Isaaks and Srivastava, 1989; Rossi et al., 1992). I computed semivariances and then fit curves to the semivariograms using the different models described above (Cressie, 1985). I used a minimum lag distance of 1-m, and active lag of 20-25-m on average (i.e., half of the minimum plot dimension). In obtaining the model fits, I had to set the active nugget, sill and range parameters using an iterative approach. The nugget is the amount of variance not accounted for in the model due to measurement error plus residual variation at distances less than the shortest sampling interval. The sill, or total sample variance, is the ordinate value at which the semivariogram becomes flat. The range represents the distance beyond which samples are spatially independent (Isaaks and Srivastava, 1989; Webster and Oliver, 2001). Nonetheless, the range for the wave semivariogram rather represents the distance beyond which samples are having a negative autocorrelation. The range, nugget and sill for each year and site were determined from each model. We obtained and analyzed a total of 72 semivariograms.

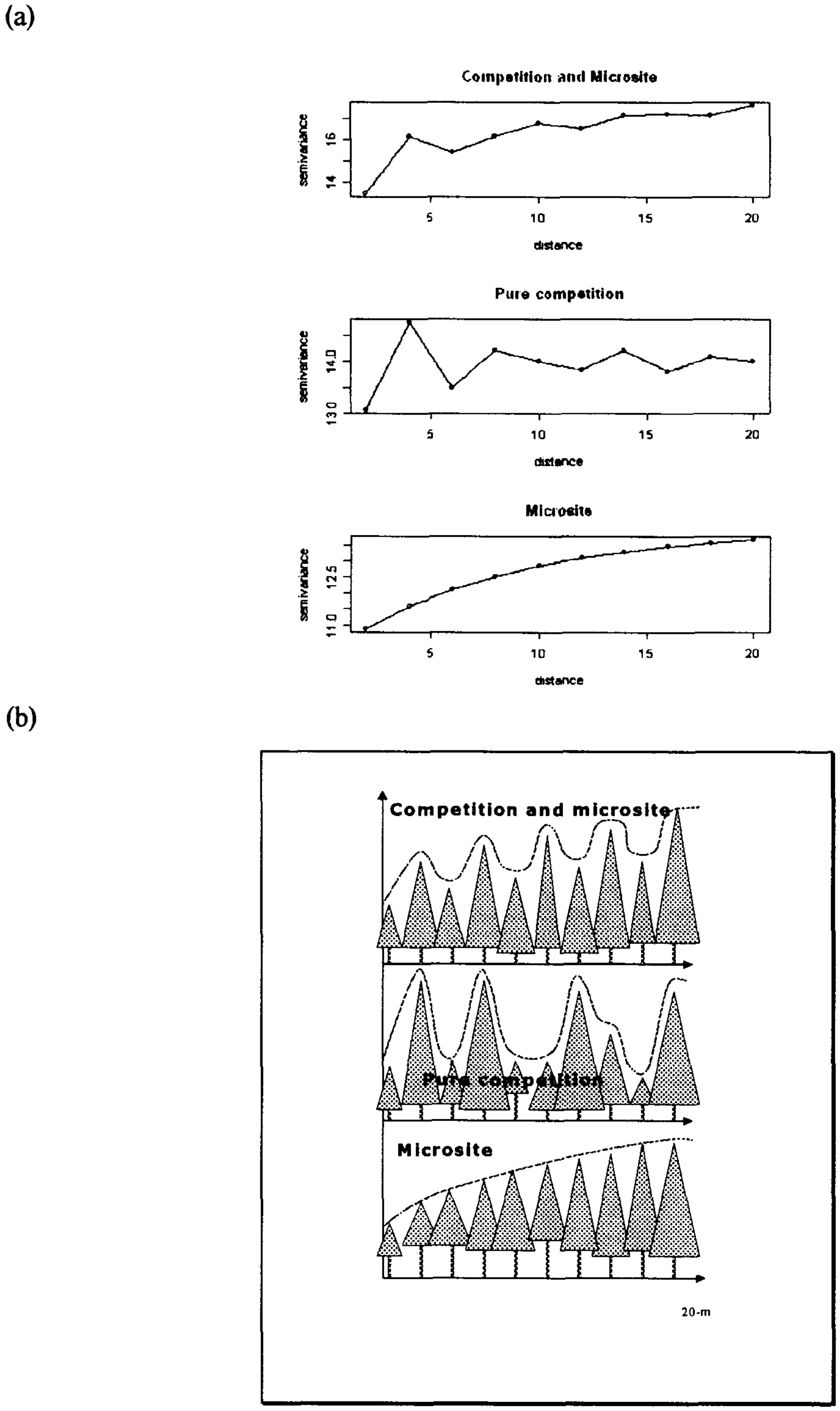


Figure 4-1. (a) Empirical semivariograms representing competition and microsite processes along with parameters used to define the model. (b) Depiction of the phenomenon among trees.

Non-linear regression (weighted least squares) with weights proportional to N(h) (the number averaged for each lag h in the semivariogram equation) was used to fit the different theoretical semivariogram models to the empirical semivariogram (Cressie, 1985). Since I used non-linear regression, least squared solutions can be sensitive to initial parameter values. Because of this, I iterated through many initial parameter values for each semivariogram, keeping the best model that has biologically meaningful parameters values for the nugget, sill and range (i.e., we rejected negative or extremely large parameter values). In cases where no least squared minimum existed within biologically meaningful parameter values (e.g., a positive nugget), I interpreted this as there being no good fit of the data to that model. In addition, each empirical RGR semivariogram was fit to the five theoretical semivariograms and relative fit was assessed using Akaike's Information Criterion (AIC) for small samples ($\mathrm{AIC_c}$) (Webster and Oliver, 2001; Burnham and Anderson, 2002). Because results depended on the entire set of candidate models, models should be identified before data analysis. Relative fit using information-theoretic statistics minimize some of the pitfalls of traditional analyses that lead to weak inference in non-experimental studies (Anderson and Burnham, 2002). A small sample version of AIC, $\mathrm{AIC_c}$, was calculated for each model with the algorithm:

$$\mathrm{AIC_c} = -2\log(\hat{\mathrm{L}}(\theta)) + 2\mathrm{K} + (2\mathrm{K}(\mathrm{K}+1)/(n-K-1))$$

where $\log(\hat{\mathrm{L}}(\theta))$ is the maximized log-likelihood value, K is the number of parameters, and n is the sample size (Burnham and Anderson, 2002). Nominally, the information criterion estimates the amount of information lost when using a particular model to approximate reality, relative to other candidate models (Welch and MacMahon, 2005): better models lose less information. It is always convenient to re-scale the $\mathrm{AIC_c}$ values such that the model with the minimum $\mathrm{AIC_c}$ has a value of 0. Thus, information-criterion values can be re-scaled as simple differences,

$$\Delta_i = \mathrm{AIC}_{ci} - \mathrm{AIC}_{cmin}$$

Then we have an estimate of the size of the increments of information loss for the various models compared to the estimated best model (the model with the minimum $\mathrm{AIC_c}$). Where $\Delta_i<2$, there is equal statistical support for the models (Burnham and Anderson, 2002). Here, I present the best and second best models. I also computed normalized Akaike weights (w_i), where each w_i provides the weight of evidence that model i is the best model (Burnham and Anderson, 2002). Empirical variograms were estimated using the "geoR" package (Ribeiro and Diggle, 2001) of the statistical software R (R-Development, 2004), as well as other model fitting in R (for variogram fitting).

4.2.4 Microsite heterogeneity: Ripley's K

In addition to the semivariogram analysis, I used the bivariate version of Ripley's K-function and its derived variable $L_{1,2}$-function (Ripley, 1977; Lotwick and Silverman, 1982), with the edge correction given in Diggle (1983). With this spatial statistic designed to estimate the spatial scale of clustering or it's opposite (repulsion), if any, I offer an alternate and pre-established method estimation of the scale of microsite variability. To do this, I assessed the spatial relationship between the lower and the upper 20% (quintile) of the annual RGR for sites Cóndor 1 and 2, separately ("lower" and "upper" data sets). For this $\hat{\mathrm{L}}_{1,2}(\mathrm{d})$ statistic, two null hypotheses are commonly used: random labeling and population independence (Goreaud and Pélissier, 2003). Since the same species is concerned, the former hypothesis was tested by comparing $\hat{\mathrm{L}}_{1,2}(\mathrm{d})$

against a 99% Monte Carlo envelope defining randomness between the two classes of trees. This procedure relied the simulated removal of trees at random from the combined ("lower" and "upper" trees) data set. The simulation was done by removing the same number of individuals as there were from the "lower" category, for example, and determining values of $\hat{L}_{1,2}(d)$ for the remaining individuals. $\hat{L}_{1,2}(d)$ values above the envelope indicate spatial attraction and values below indicate spatial repulsion (i.e., spatial separation) between the two classes of trees (Lotwick and Silverman, 1982). The spatial statistics program SPPA.EXE (Haase, 2002) was used.

4.3 RESULTS

4.3.1 General stand characteristics and spatial autocorrelation

Basal area at breast height (BA) varied among sites from 5.36 to 29.38 $m^2 * ha^{-1}$ (Table 4.1). I found a striking difference in BA and mean height between the Mirador and Flamenco stands. This difference was accentuated by considering that the Flamenco stand was planted 6 years earlier than the Mirador stand. From these results I can suggest the existence of a marked difference in site quality between the Flamenco (poor site) and Mirador stands. Although the Cóndor 1 and 2 sites have not experienced artificial thinning, their densities have decreased from the original 1666 trees per hectare (3 x 2 planting arrangement) by approximately 10 and 30% in Cóndor 1 and 2, respectively. The densities after thinning also varied in the other sites. Flamenco 1 and 2, for example, had approximately 60% of density decreasing. Spatial autocorrelation of individual tree RGR was strongly detected across all sites as most of the semivariograms obtained were significantly different from just nugget spatial effects (but see the early years in the

Mirador and Flamenco stands). At least one of the semivariogram models proposed explained well the spatial RGR variability (Table 4.2).

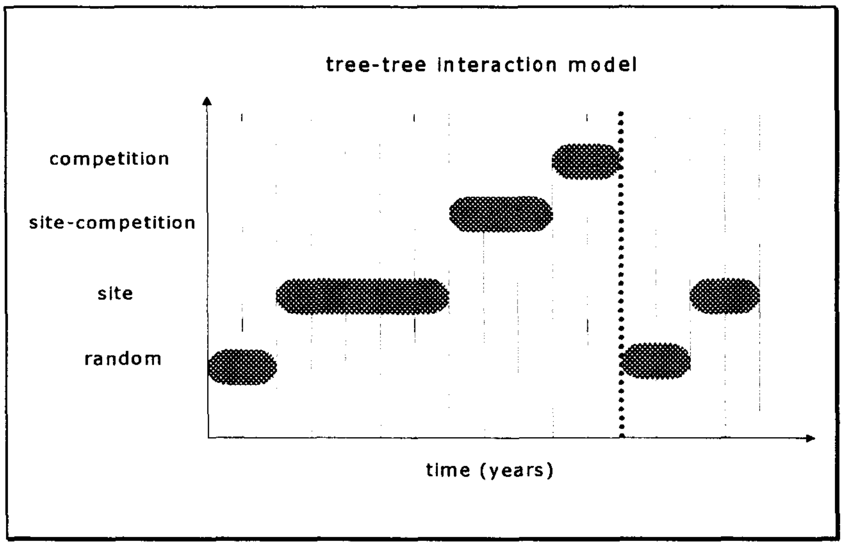


Figure 4-2. General model proposed to depict tree-tree interaction processes through time (stand development) inferred from spatial patterns in uneven-aged mono-specific plantations. Discontinuous line in bold represents the eventual application of thinning.

Table 4-1. Stand descriptions corresponding to 2004 by site for even-aged ponderosa pine plantations in Patagonia, Chile. One-unit standard errors for height are in parenthesis.

Sites	Planting year	Thinning year	BA (m^2/ha)	Mean height (m)	Density (#/ha)
Cóndor 1	1993		9.62	4.2 (0.05)	1382
Cóndor 2	1993		5.36	3.7 (0.06)	1139
Mirador 1	1987	2001	22.92	6.0 (0.06)	906
Mirador 2	1987	2001	29.38	6.6 (0.08)	933
Flamenco 1	1981	1998	8.57	4.9 (0.08)	414
Flamenco 2	1981	1998	12.59	5.2 (0.11)	532

Note: BA stands for basal area at breast height.

4.3.2 The intraspecific interaction model

In general, spatial patterns of individual-tree RGRs followed the predicted model for intraspecific interactions in the three tree populations. Early years exhibited no spatial patterns (lack of autocorrelation), followed by microsite effects (except in the Mirador sites). In addition to these two patterns, the competition model was supported in all the sites, both combined with microsite effects and/or as pure competition effects. Artificial thinning broke this competition signal, which developed either towards a lack of autocorrelation (Mirador 2, Flamenco 1 sites) or microsite effects (Mirador 1, Flamenco 2 sites). As expected, the unthinned sites presented significant differences in RGR from the thinned ones, likely due to both the thinning practice applied, and the stand development stage they represented, and perhaps differences in site quality (Figure 4.3). For the Mirador sites, there was evidence of strong competition just before the site was thinned (particularly for Mirador 2). Surprisingly, there was also support for early competition at both Mirador sites (around 1994). This event was followed by a release from competition. The Flamenco 1 site exhibited a succession of effects that matched very well with the predicted population development model. Even though the Flamenco 2 site showed competition effects just before thinning, I found a strong prevalence of microsite effects for periods both before and after thinning. For some particular years, an overlap between the best and the second best model depicting the prevailing process of such a year was detected (Figure 4.3). This may suggest the existence of a transitional period between the prevalence of microsite and competition processes or simply model uncertainty (Burnham and Anderson, 2002).

4.3.3 Microsite heterogeneity: Ripley's K

I found that individual trees belonging to the "lower" data set had a negative spatial association when compared to the upper quintile annual RGR, particularly for later years in the two unthinned sites (Table 4.4 and Figure 4.4). For the Cóndor 1 site, this spatial distinction between both RGR classes is consistent throughout all scales. For the Cóndor 2 site, the scale of repulsion reached a maximum of 10-m. This clear spatial distinction between extreme-case performances corroborates the existence of microsite patches that differ in quality. These results also match the range values for spherical semivariogram models (microsite), corroborating the scale of patches.

Table 4-2. Summary of AIC selection models, Akaike differences, and Akaike weights (*wi*) for describing tree-tree interactions in ponderosa pine plantations.

		Model Support									
		Wave (3)		Nested (5)		Spherical (3)		Exponential (3)		Nugget (1)	
Site		Δ_i	w_i	Δ_i	w_i	Δ_i	w_i	Δ_i	w_i	Δ_i	w_i
Cóndor 1	2003			0.000	0.892						
	2002			1.269	0.203	0.000	0.382	1.083	0.223		
	2001	0.355	0.414	0.000	0.494						
	2000			0.000	0.484			1.784	0.198		
	1999			1.847	0.190	0.000	0.479	0.738	0.331		
	1998					0.000	0.558	1.242	0.300		
	1997					0.000	0.656	1.650	0.287		
Cóndor 2	2003			0.000	0.512	1.250	0.274				
	2002			0.000	0.738						
	2001			1.859	0.171	0.000	0.434	0.382	0.359		
	2000			0.000	0.946						
	1999			0.378	0.287	0.134	0.325	0.000	0.347		
	1998					0.000	0.989				
	1997									0.000	0.999
Mirador 1	2003			1.466	0.152	0.234	0.281	0.000	0.316		
	2002			1.845	0.115	0.000	0.291	0.323	0.248		
	2001			0.000	0.708						
	2000	0.000	0.481			0.979	0.295	1.701	0.205		
	1999			0.000	0.616						
	1998			0.000	0.462	0.955	0.286				
	1997			0.000	0.685						
	1996					0.000	0.459	0.633	0.335		
	1995									0.000	0.406
	1994	0.000	0.413	0.976	0.253					0.777	0.280
	1993	0.460	0.386							0.000	0.485
	1992									0.000	0.611
Mirador 2	2003			1.746	0.215	0.000	0.516	1.338	0.264		
	2002									0.000	0.674
	2001	0.000	0.321			0.575	0.240	0.699	0.226		
	2000	0.000	0.685								
	1999	0.000	0.464					1.769	0.192		
	1998			0.000	0.345	0.401	0.282	0.505	0.268		
	1997	1.607	0.213			0.000	0.476				
	1996			0.000	0.887						
	1995	1.389	0.295							0.000	0.590
	1994	0.000	0.614							0.282	0.173
	1993	0.180	0.401							0.000	0.438
	1992									0.000	0.474
Flamenco 1	2003					0.000	0.503	0.740	0.348		
	2002					0.000	0.548				

	2001									0.000	0.870
	2000									0.000	0.870
	1999					1.080	0.294			0.000	0.504
	1998	0.348	0.331	0.000	0.394						
	1997			0.000	0.667						
	1996					0.000	0.489	0.300	0.421		
	1995			1.639	0.185	0.000	0.419	0.113	0.396		
	1994			0.000	0.945						
	1993			0.704	0.283	0.503	0.313	0.000	0.403		
	1992							0.000	0.645		
	1991					0.000	0.376	0.225	0.337		
	1990	0.479	0.388							0.000	0.493
	1989									0.000	0.733
	1988									0.000	0.999
	1987									0.000	0.999
Flamenco 2	2003					0.000	0.424	0.410	0.345		
	2002			0.415	244	0.428	0.242	0.000	0.300		
	2001					0.000	0.448	1.547	0.206	0.734	0.310
	2000			0.585	0.260	0.000	0.349	0.065	0.337		
	1999					0.000	0.546	1.430	0.267		
	1998	0.000	0.727								
	1997			0.487	0.346	0.000	0.441	1.776	0.182		
	1996					0.000	0.561	1.935	0.214		
	1995					0.000	0.697				
	1994					0.000	0.938				
	1993					0.000	0.815				
	1992					0.000	0.858				
	1991					0.000	0.860				
	1990					0.000	0.755				
	1989	1.750	0.205			0.052	361	0.000	0.371		
	1988									0.000	0.413
	1987									0.000	0.891

4.4 DISCUSSION

This study demonstrated that stochastic patterns can be usefully decomposed in more deterministic causes, named competition and microsite, which led us to determine when these processes prevail based on the spatial individuals' performance (and variation) in a population. The distinction and quantification of these processes' strength in time and space might be of the greatest importance for decreasing inaccurate predictions in individual-based modeling (Pfister and Stevens, 2003) and hence, improving population projections. These results suggest that competition, expressed as an abrupt difference in annual RGR between neighboring trees, was detected to occur mostly *after* microsite resource effects had been accounted for as the prevalent process. Based on these results, the stand development model worked well for the relatively young ponderosa pine plantations used to test it, where: first, I was able to corroborate the presence and scale of microsite variability (based on L-function); second, each site progressed through a reasonable sequence of patterns; and third, it nearly perfectly detected the presence of artificial thinning (we could tell from our analysis when thinning occurred, without external knowledge).

Table 4-3. Weighted semivariogram range coefficients for the 5 models, representing the spatial pattern of tree-tree interactions in even-aged ponderosa pine populations, Patagonia, Chile.

Site	Year	Ranges					
		Nested-wave	Nested-exp	Exponential	Spherical	Wave	Best model
Cóndor 1	1	1.18	4.09	13.46	19.50	2.76	Nested
	2	2.66	10.97	7.49	16.81		Spherical
	3	2.63	9.76	3.72	15.24	2.63	Nested
	4	2.63	4.11	2.40	9.58	1.96	Nested
	5	1.77	4.19	4.99	11.46	1.17	Spherical
	6	5.47	6.95	2.00	8.02	1.55	Spherical
	7			1.13	4.12	4.98	Spherical
Cóndor 2	1	3.54	4.69	13.76	12.69		Nested
	2	3.05	8.41	3.97	12.65	13.17	Nested
	3	4.61	4.91	17.20	16.79		Spherical
	4	4.26	2.21	3.33	10.88	2.32	Nested
	5	1.13	11.22	9.37	17.18	1.12	Exponential
	6				2.91		Spherical
	7				3.05	1.52	Nugget
Mirador 1	1	5.13	23.32	4.78	9.37	1.85	Exponential
	2	1.40	3.55	2.93	7.24	1.23	Spherical
	3	2.46	2.94	8.58	10.39	2.45	Nested
	4			18.01	19.37	0.93	Wave
	5	1.86	4.53	7.65	16.36	1.88	Nested
	6	4.25	2.37	4.84	12.07	1.13	Nested
	7	2.36	15.05	36.20	18.59	0.10	Nested
	8			7.67	16.47	2.95	Spherical
	9			2.23	5.38	3.73	Nugget
	10	3.71	0.84	5.80		1.37	Wave
	11	2.24	4.81	5.35		1.16	Nugget
	12	2.93	1.48	3.22	9.84		Nugget
Mirador 2	1	2.62	1.93	2.60	8.12	1.33	Spherical
	2			2.15		2.42	Nugget
	3			8.02	11.16	2.66	Wave
	4			1.29	5.31	1.21	Wave
	5	3.56	1.14		4.35	2.63	Wave
	6	2.05	25.44	36.11	32.26		Nested
	7	2.51	2.57		3.44	2.51	Spherical
	8	3.21	0.82	2.31		3.18	Nested

	9	2.71	1.18	2.00		1.21	Nugget
	10	2.73	2.81	2.61	7.36	2.72	Wave
	11	2.18	5.18	6.75		0.69	Nugget
	12	3.07	16.89	11.26		1.33	Nugget
Flamenco1	1			26.19	29.99		Spherical
	2	1.84	29.97	30.82	31.16		Spherical
	3				4.55		Nugget
	4			96.89			Nugget
	5			1.70	6.21		Nugget
	6	1.19	5.41	30.33			Nested
	7	1.28	20.49	68.15	35.24	3.70	Nested
	8	1.60	29.03	41.32	29.21		Spherical
	9	3.54	28.80	54.54	39.08		Spherical
	10	2.20	29.67	34.98	33.03	1.18	Nested
	11	2.18	21.46	22.98	30.61		Exponential
	12	3.05	9.69	10.41	23.44	0.57	Exponential
	13	1.21	8.89	22.23	24.56		Spherical
	14	3.65	1.23			1.16	Nugget
	15						Nugget
	16						Nugget
	17						Nugget
Flamenco 2	1	2.73	1.84	1.60	7.38		Spherical
	2	1.38	1.39	2.94	10.71		Exponential
	3	2.78	4.59	4.83	16.40		Spherical
	4	1.29	5.45	2.44	6.21	2.61	Spherical
	5	2.58	17.45	14.67	25.93	3.19	Spherical
	6	2.40	1.10			2.40	Wave
	7	1.19	4.20	8.11	18.94		Spherical
	8	2.66	8.24	6.58	17.96		Spherical
	9	1.17	7.08	11.40	22.28	2.62	Spherical
	10	1.46	5.01	6.33	16.75		Spherical
	11	0.45	7.09	9.43	20.92	2.23	Spherical
	12			7.96	19.85		Spherical
	13			11.23	22.87	3.24	Spherical
	14	1.19	5.42	7.64	18.43		Spherical
	15	3.78	9.25	14.63	25.16		Exponentiall
	16	2.62	1.41	1.96	7.42	2.62	Nugget
	17	2.28	2.29	5.13			Nugget

Note. All range semivariogram coefficients that are not showed were biologically meaningless.

As evident in Figure 4.3, some overlap between both microsite and competition processes could be detected. This event was expected, given that more than one underlying process may be operating simultaneously (Wyszomirski et al., 1999), which in ecology is very plausible (Hilborn and Stearns, 1982; Burnham and Anderson, 2002). Furthermore, these overlapping processes may represent a transitional period during which both processes can be operating. During these transitional periods we can expect that trees belonging to different RGR classes will be at different stages in the competition process (Reynolds and Ford, 2005), because of microsite differences between "good" and "worse" patches (see Figure 4.4 for Cóndor 1 and 2). The existence of microsite patches in the resource availability was detected (spatial point pattern analysis), in which varying degrees of competition intensity may have been occurring. The development of size hierarchies have mostly been attributed to asymmetric competition (Stoll et al., 2002), however, at stand or plot level, they may also be the result of a patchy resource distribution (Wilson and Gurevitch, 1995). Thus, microsite variation is an important factor altering process development. It is often assumed that site (but not microsite) quality can determine the outcome of competition, provided that multiple resources limit growth, and that competitive hierarchies change across a gradient of resource availability. Nonetheless, this assumed trend for competition delay, in the case of poor quality sites (Grime, 2001), can also be detected at smaller scales, i.e., at the plot level, where there may be poorer resource-quality spots for tree growing. For example, we found a clear negative spatial association between the upper and lower quintile of annual RGR at both unthinned sites Cóndor 1 and 2. This pattern indicated the existence of two different zones in the plots: one where the lower quintile of annual RGR individuals is located, and another where the upper quintile of annual RGR individuals is located. It is possible that trees belonging to the upper quintile of annual RGR started to compete among themselves earlier than trees of the lower quintile. If this is the case, this phenomenon may potentially obscure the appearance of the expected spatial pattern (i.e., competition) for a specified sample unit size. Additionally, the scale at which these two RGR-classes were negatively associated was in accordance with the range values found for the spherical models (Table 4.3 and 4.4). These similar results coming from two different spatial approaches show the importance of considering microsite patches. I also found that this spatial distinction between extreme RGR-class trees was based on microsite quality differences only, and not related to competition processes *per se*; competitive interactions experienced by an individual occur at a very local scale (Benjamin and Hardwick, 1986; Huston and DeAngelis, 1987; Hara, 1988; Gurevitch et al., 2002). Therefore, it is improbable that a mean lower quintile RGR tree is being outcompeted by a tree belonging to the upper quintile RGR. Tree-interactions typically are restricted to a subset of neighboring individuals and the likelihood that two plants will interact can be viewed as a decreasing function of the distance between them (Stoll and Weiner, 2000). I found that competition and microsite (nested model) were the prevalent processes observed (Figure 3); however the level or intensity of the competition process may vary depending on the quality of the microsite. Prior to the current study, it has been very difficult to separate the effects of these two processes (Turkington and Aarssen, 1984) in leading to the repulsion of upper and lower RGR trees.

As the model predicted, the evidence for spatial interactions between neighbors depended strongly on the population development stage (Gurevitch et al., 2002), which accentuates the importance of having a dynamic overview of the interaction process rather that static one (snap-shot-like). Oliver (1981) described and formulated a tree population development model for natural even-aged tree populations that follows stand-replacement disturbances events. His model established four main sequential stages in stand development: first, initiation; second, exclusion or self-thinning; third, understory reinitiation or mature; and fourth, old-growth. Plantations with fast-growing tree species in favorable sites (e.g., ponderosa pine in Patagonia) may represent a synthetic representation of Oliver's model in time. Further studies would be necessary to evaluate whether this intraspecific tree interaction model based on the spatial autocorrelation approach performs well in natural forest populations.

Table 4-4. Patterns of spatial association between the lower and upper quintile of annual RGR, for trees at sites Cóndor 1 and 2 of ponderosa pine plantations in Patagonia, Chile.

Site	Cóndor 1																	
		Lower vs. upper quintile of annual RGR																
Year	n_1/n_2 †	Distance t (m) *																p¶
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
2003	58/58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01
2002		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01
2001				-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01
2000																		.92
1999																		.92
1998				-	-	-	-											.42
1997		-	-	-	-	-	-	-	-	-								.05

Site	Cóndor 2																	
		Lower vs. upper quintile of annual RGR																
Year	n_1/n_2	Distance t (m)																p
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
2003	38/38	-	-	-	-	-	-	-	-	-								.04
2002		-	-	-	-	-	-	-	-	-	-							.03
2001		-	-	-	-	-	-	-	-	-								.02
2000						-	-	-	-	-								.05
1999						-	-											.15
1998																		.71
1997																		.37

† n_1 stands for the number of individuals in the plot belonging to the lower 20% annual RGR; n_2 corresponds to the upper 20% annual RGR. They are similar for all the years.

* The symbol + indicates significant positive association; - indicates significant negative association at distance t, based on $L_{1,2}(t)$-function. No symbol indicates independence.

¶ Significance is evaluated using a 99% Monte Carlo confidence interval (99 simulations) with a 1-m step. The Cramer-von-Mises test was used to test for overall significance of patterns over the complete range of t, with p-values reported in the column titled "p".

4.4.1 Thinning scenario

One of the tests of the success of the current approach was to assess whether I was able to reproduce the timing of the known artificial thinning events. The model successfully detected competition before thinning and an abrupt loss of competition at all sites following thinning. This was detected even though I was only able to consider the remnant trees (i.e., many of the stand level data were lost in the thinned trees). Thus, the biological processes emerged in the spatial patterns in spite of the loss of data due to thinning.

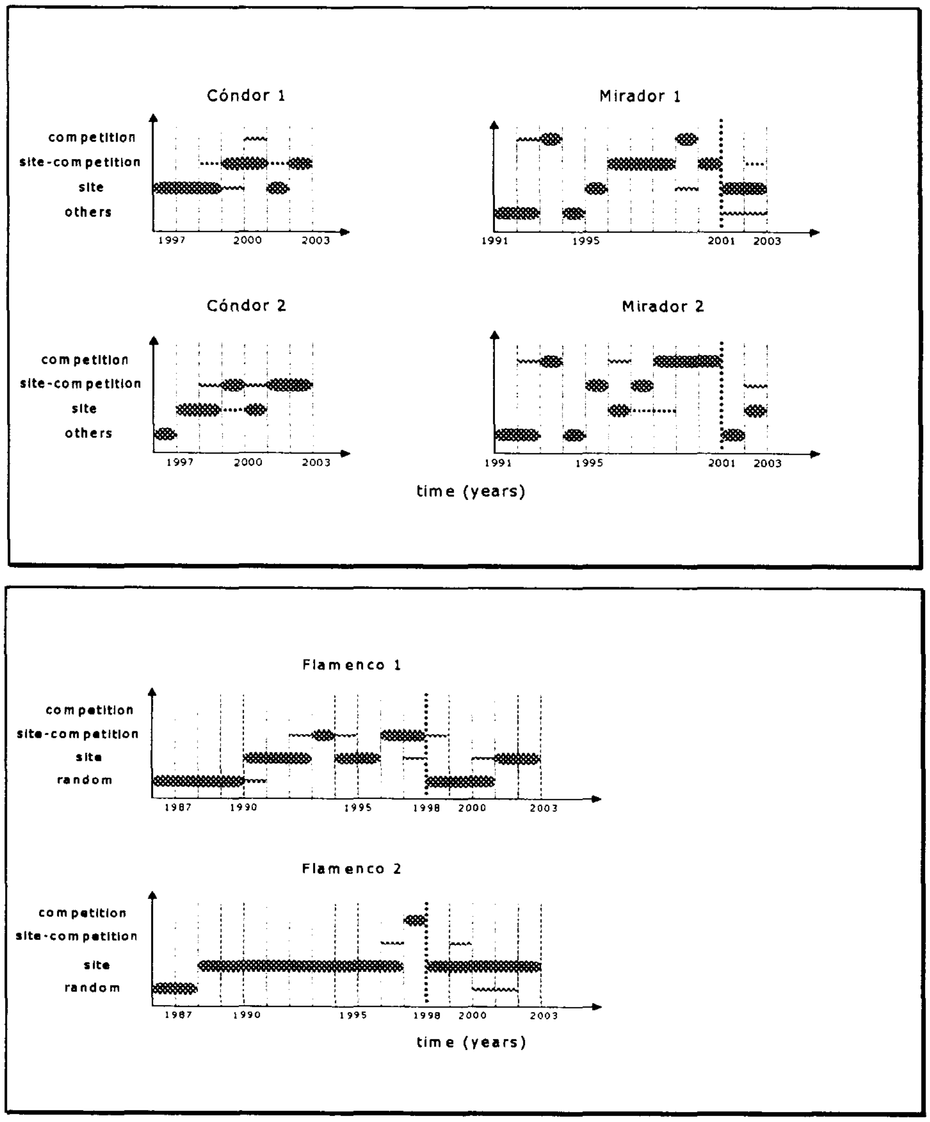


Figure 4-3. Tree-tree interaction models obtained from spatial patterns (using semivariograms) found in even-aged ponderosa pine plantations in Patagonia, Chile. Thick stripes represent the best model (lowest AICc). Thinner stripes represent the second best model within a range of 2 units. Dotted lines in bold represent the time when thinning was applied.

Because of the biological inference gained in this study, I was able to infer the actual type of thinning that occurred (as I did not know before this study if the thinning was applied in a random way or targeted just towards small size classes). Thinning that resulted in microsite-specific growth (e.g., Flamenco 2) suggests that thinning targeted smaller trees, breaking up tree-tree interactions, but not the underlying microsite effects that are most prominently detected by the dominant trees. Thinning that creates a random spatial pattern (e.g., Flamenco 1) implies that the thinning broke up tree-tree interactions, as well as microsite-specific growth, suggesting that thinning was more random.

4.4.2 Final remarks

Overall, the current semivariogram approach based on the *a priori* intraspecific tree interaction process hypotheses performed as expected, and therefore may provide guidance and insights as to when and how individual variation is altered by different processes. I was able to disentangle both competition and microsite effects based on the spatial pattern signature of the tree RGRs exhibited. Few other attempts have been conducted toward this end. Bachacou and Decourt (1976) were pioneers in incorporating a geostatistics approach based on DBH semivariograms to tease potential processes apart. However, they used just a couple of years to account for the dynamics of their Douglas-fir stands, and they did not use an objective criterion (e.g., AIC) to distinguish among multiple competing models. By using RGR, I chose a rather conservative measure to detect competition (Ford, 1984; Hunt, 1990; Gurevitch et al., 2002). Since there were likely initial differences in seedlings size, therefore the use of an absolute measure (BA, DBH) would have biased the interpretation of actual competition: detecting competition where there was not interaction. A possible drawback of this analysis technique is the added effort and expense that is required to obtain the spatially referenced data. This is a common drawback of distance-dependent, individually-based models and competition indices (Wimberly and Bare, 1996; Courbaud et al., 2001). However, I consider this approach to be an improvement relative to individual-tree models based on competition indices only, because it incorporated microsite heterogeneity as an important component explaining individual tree growth. Besides, competition indices generally do not account for the spatial dependency of observations.

The approach I present here, analyzing the spatial pattern of a measurable feature (e.g., growth rate) as a surrogate for direct measures of an ecological process (e.g., competition), provides a potential analysis approach whenever researchers cannot directly measure the process of interest. As most ecological data are not spatially independent (Legendre, 1993), ecologist can model the spatial variability that characterizes each set of data and attach to specific processes. Even though, there is a limited set of semivariogram models, like the linear, the spherical, the exponential, the Gaussian, to name only those that are most frequently used, with further processing (the nested model) and constraints (in the range parameter), we can still represent a fair number of ecological processes.

Ultimately, the establishment of general patterns that relate resource availability and competition intensity has been controversial in population and community ecology (Gurevitch et al., 2002; Boyden et al., 2005). It has been stated that an improvement in the representation of intraspecific interactions is needed (Reynolds and Ford, 2005). Such an improvement will require the use of individual-based models that explicitly represent size variation, resource acquisition, two-dimensional stand distribution, and dynamic (rather than static) stand or individual resource utilization (Reynolds and Ford, 2005). I believe that with this semivariogram approach I have explicitly incorporated the main components required for a better understanding of the observed performance variation; dynamic relationships between microsite variation and competition onset, under a spatial and temporal framework in a plant population.

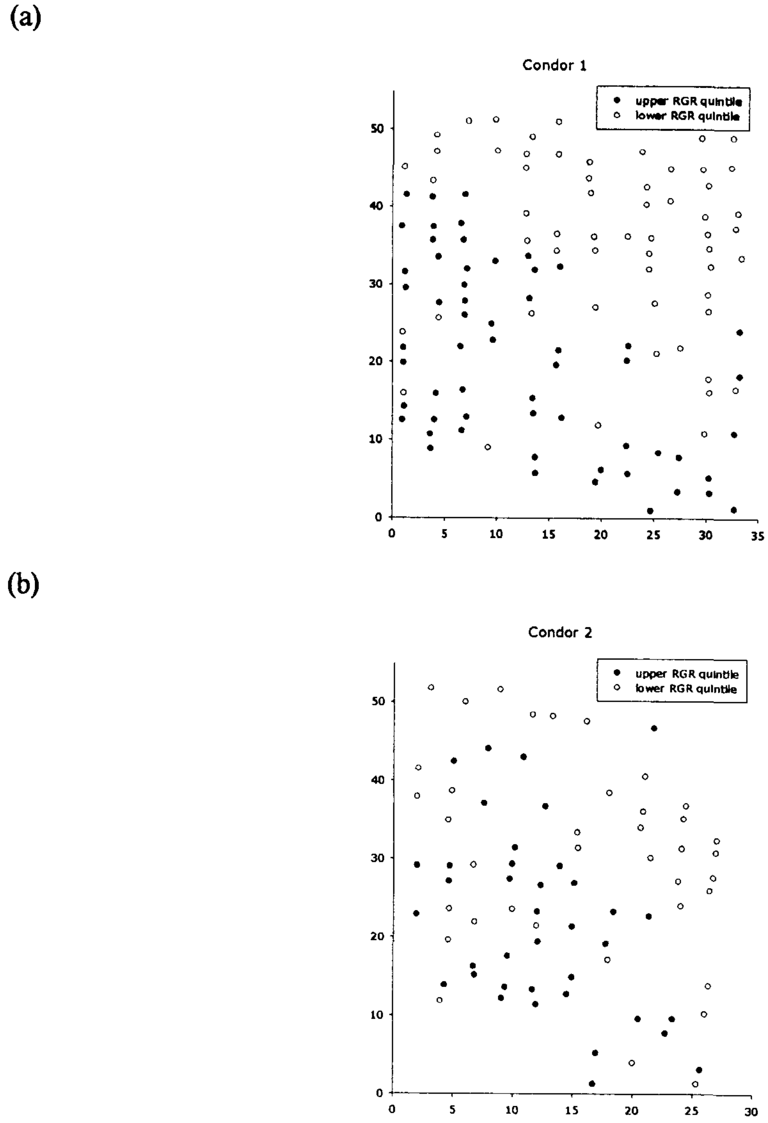


Figure 4-4. Stem-maps for the upper and lower RGR quintile (20%) at (a) Cóndor 1 and (b) Cóndor 2 in even-aged ponderosa pine plantations in Patagonia, Chile.

Chapter 5

MID-TERM RESPONSES OF FOREST RESTORATION PRACTICES ON THE GROWTH, VIGOR AND RECRUITMENT OF PONDEROSA PINE IN THE LICK CREEK EXPERIMENTAL AREA, BITTERROOT NATIONAL FOREST, MONTANA

> "The practice of ecological restoration has been identified as providing ideal experimental settings for tests of ecological theory; restoration was to be the 'acid test' of our ecological understanding" (Young et al., 2005).

5.1 INTRODUCTION

In recent years, large scale stand-replacing wildfires have played an increasing role in influencing the structure and function of temperate coniferous forests across the Inland Northwest (Smith et al., 2005; Smithwick et al., 2005). However, prior to Euro-American settlement, natural disturbance dynamics of lower elevation ponderosa pine forests in the Rocky Mountains were primarily driven by frequent but low intensity surface fires that tended to maintain open, multi-aged, and biologically diverse stands (Arno, 1988; Agee, 1993; Covington and Moore, 1994; Mast et al., 1999). In the northern Rockies, understory burns limited more shade-tolerant competitors, particularly Douglas-fir, from developing in the understory and eventually replacing ponderosa pine (Thomas and Agee, 1986; Fiedler, 2000; Hartwell et al., 2000). In the last century, however, fire exclusion practices have changed the dynamics of these forest ecosystems.

An increase in understory biomass dominated by shade-tolerant species, along with a decrease of ground flora structure and diversity have been cited as the most striking changes (Arno et al., 1995a; Mast et al., 1999; Moore et al., 1999). The increased stocking levels (particularly in the understory) have increased competition for resources, the risk of insect and disease outbreaks, and the potential for stand replacing fires (Fulé et al., 1997; Feeney et al., 1998; Keane et al., 2002). Because of these adverse effects, active management using prescribed fires and harvest/thinning are increasingly used to partially restore historical conditions and reduce the risk of stand replacing crown fires (Arno et al., 1995a; Powers and Reynolds, 2000; Fiedler et al., 2003; Smith et al., 2005). Managers have justified this decision by assuming that presettlement conditions and processes may best represent factors that shaped the evolution of these forest communities (Covington et al., 1997; Moore et al., 1999). How these ponderosa pine forests will respond to restoration practices is sometimes difficult to predict.

Various studies have dealt with restoration response, but the conclusions have been somewhat contradictory (Suding et al., 2004). Practices such as thinning and prescribed fires have been evaluated based on tree growth and mortality (Fiedler, 2000), as well as on changes in nutrient cycles and understory vegetation structure (Arno et al., 1996; Monleon et al., 1997; Kaye and Hart, 1998; Busse et al., 2000; DeLuca and Zouhar, 2000; Gundale et al., 2005; Sala et al., 2005; Smithwick et al., 2005). In some studies, thinning followed by burns has resulted in increased soil water availability and improved physiological performance for second-growth (Skov et al., 2004; Sala et al., 2005) and old-growth ponderosa pine (Feeney et al., 1998). However, in other studies a reduction of growth rates and increased mortality have also been reported following prescribed burns (Swezy and Agee, 1991; Landsberg, 1994; Busse et al., 2000). Most of these studies were conducted in second-growth stands and therefore did not specifically evaluate the response of different age cohorts to restoration practices (but see McDowell et al. (2003) and Skov et al. (2005)).

Current ponderosa pine restoration practices are often conducted in part to reduce catastrophic fire hazard, but another objective has been to improve individual tree vigor, particularly for the conservation of older trees left in the stand (McDowell et al., 2003; Skov et al., 2005). Improvement in vigor can potentially decrease the vulnerability of these older trees to attacks by insects and pathogens (Mitchell et al., 1983; Coyea and Margolis, 1994). One useful index of tree vigor is the physiologically-based measure of growth efficiency, which is the amount of stemwood production per unit leaf area (Waring, 1983; Coyea and Margolis, 1994). Growth efficiency (GE) reflects the average capacity of a tree crown to assimilate carbon, assuming that allocation to stemwood occurs as a lower priority than other allocations to defensive compounds and starch storage (Waring and Running, 1998). Growth efficiency has also been examined to measure intensity of competition among individual trees (Mitchell et al., 1983; Waring and Running, 1998), and has been increasingly applied in studies related to tree and stand growth (Smith and Long, 1989; O'Hara, 1996; Seymour and Kenefic, 2002). It has generally been found that GE decreases with increasing tree size and age (Maguire et al., 1998; Waring and Running, 1998; Seymour and Kenefic, 2002), but this also varies with stand structure and the crown class of individual trees (Maguire et al., 1998; Binkley et al., 2002; Woodall et al., 2003). Little is known, however, regarding the potential for restoration practices to promote the growth and vigor in treated stands, particularly in older individuals (Latham and Tappeiner, 2002; Skov et al., 2005).

In ponderosa pine forests that historically experienced frequent, low-intensity surface fires, restoration efforts aimed at conserving older trees generally take uneven-aged silvicultural approaches (Smith et al., 1997). Multi-aged silvicultural practices (i.e., selection harvests) consider both the maintenance of vigorous growth on the reserve growing stock (e.g., older trees) and the recruitment of a new age-class (O'Hara, 1996; Smith et al., 1997). Few studies have examined how individual tree selection and subsequent prescribed burning affect the species composition of regeneration (Bailey and Covington, 2002). If one of the goals of these practices is to restore presettlement forest composition, recruitment of seral ponderosa pine regeneration following treatments is another key measure for assessing success of restoration efforts. Better quantitative data on recruitment of desirable regeneration could help in the evaluation of alternative treatments and promote the adoption of effective restoration practices (Brandeis et al., 2001).

In this study, my general aim was to examine the effects of restoration treatments on growth, tree vigor and post-treatment seedling recruitment in low-elevation ponderosa pine in western Montana. Specifically, I compared basal area increment and growth efficiency of overstory trees, as well as the abundance of recruited seedlings 10 years after the implementation of two restoration treatments, relative to an untreated control. Restoration treatments were conducted using modified selection cutting with and without prescribed burning. I addressed the following questions: 1) Is there a significant growth response of reserve trees following restoration treatments, both in terms of increased basal area increment and improved tree vigor (as indexed by growth efficiency)? 2) What is the effect of including Spring prescribed burns with restoration thinning on the growth and vigor of reserve trees? 3) Do various age-classes of trees respond differently to restoration treatments? 4) Can restoration harvests be effective at increasing vigor of older trees? 5) Does the addition of spring prescribed burns to restoration harvests increase the relative abundance of seral ponderosa pine? 6) Are seedling recruitment levels spatially associated with local stand and site characteristics?

5.2 STUDY AREA AND METHODS

5.2.1 Study site and restoration experimental design

The study was undertaken in the Lick Creek Experimental Area in the Bitterroot National Forest of western Montana (46°5' N, 114°15' W), at an elevation of ca. 1500 m. The annual precipitation in this area averages 500 mm, about half of which falls as snow (Gruell et al., 1982). The site is dominated by ponderosa pine that range in age from 20 to 250 years of age, with a small component (<10% of total basal area) of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco) that tended to be younger in age.

Restoration treatments were applied in 1992 and 1993. Trees were harvested using single-tree selection harvests in the fall of 1992 and randomly selected units were broadcast burned in the spring of 1993 (DeLuca and Zouhar, 2000). Nine study units, one hectare each, were established in three blocks (replicates) adjacent to each other in a completely randomized experimental design of two treatments and one control. Six units received a stand basal area reduction treatment via selection harvests; prescribed burning was applied to three of these (Harvest-Burn), while the other three remained unburned (Harvest-only). Three units were left un-harvested and unburned to serve as controls (Control). Restoration targets for these stands were based on investigations of old-growth ponderosa pine in western Montana. Modified, single-tree selection harvests reduced pretreatment stocking levels from 23 m^2*ha^{-1} (in trees >10-cm) to a target reserve basal area of 11 m^2*ha^{-1} for each of the six 1-ha treatment units. In all units, trees intended to remain were tagged. Within uncut controls, these tagged trees provided a comparable set of reserve trees to those left in treated units, in terms of initial size and crown class distribution. The total basal area (BA) within the ~0.3-ha sampled plots of the treated units (Harvest-only and Harvest-Burn) ranged from 6.9 to 12.7 m^2*ha^{-1} (Table 5.1). Tagged trees within the 0.25-ha untreated Control units had similar range (9.1 to 10.3 m^2*ha^{-1}), while total basal area of all trees ranged from 14.2 to 20.3 m^2*ha^{-1}. The tree density varied from 127 to 237 $trees*ha^{-1}$ for plots in Harvest-only and Harvest-Burn units, and from 110 to 152 tagged $trees*ha^{-1}$ in Control units (312 to 348 $trees*ha^{-1}$ total).

5.2.2 Field data collection

In summer 2003, I established one square plot (50x50 to 60x60-m) in the center of each experimental unit for stem mapping all trees > 10-cm in diameter at breast height (DBH; 1.37-m high). For stem maps, the distance and azimuth to the center of each tree (>1.37-m tall) within experimental units were measured using a laser rangefinder (Impulse™) equipped with a MapStar™ electronic compass module (Laser Technology Inc.) leveled on a surveyor tripod. These field measurements were converted to Cartesian coordinates using trigonometric functions. For all trees > 10-cm DBH, we measured DBH and extracted an increment core to the pith at DBH using an increment borer. For trees larger than 20-cm DBH, two such cores were extracted. Sapwood-heartwood boundaries were visually identified on each increment core in the field. When the boundary was difficult to determine, bromecresol green was used to stain the sapwood (Kutscha and Sachs, 1962).

Table 5-1 Summary of stand characteristics by experimental unit in the Lick Creek Experimental Area of western Montana 10 years after treatments were applied. Basal area and density correspond to residual trees only (see footnote). Data for ≥ 0.25-ha plots were scaled up to per hectare basis. Seedlings represent seedlings recruited after treatments were applied.

		Basal Area (m^2*ha^{-1})				Density (trees*ha^{-1})				Seedlings (#*ha^{-1})		
Block	Treatment	Young	Mature	Preset.	Total	Young	Mature	Preset.	Total	PP	DF	Total
1	H¶	1.11	4.87	2.48	8.46	140	83	13	236	33	127	160
	HB	0.11	8.41	3.05	11.57	11	125	8	144	67	156	222
	C	0.17	7.04	5.12	10.33	24	84	24	132			
	C*	0.20	11.42	7.21	18.83	28	248	52	328	7	117	123
2	H	0.49	8.82	1.65	10.96	25	114	6	145	86	8	94
	HB	0.36	5.98	0.64	6.98	27	110	3	140	87	97	183
	C	0	5.51	3.63	9.14	0	120	20	140			
	C*	0.12	9.23	4.95	14.30	4	272	36	312	4	8	12
3	H	0.20	3.92	5.36	9.48	7	73	47	127	33	87	120
	HB	0.25	7.55	4.90	12.70	11	100	26	137	47	50	97
	C	0.57	3.93	5.09	9.59	32	80	40	152	3	10	13
	C*	1.01	5.60	13.74	20.35	72	128	148	348	3	10	13

¶ H = Harvest-only; HB = Harvest-Burn; C = tagged trees only within uncut Controls; C* = all trees within uncut Control. Trees were tagged within uncut Control at time of treatments to provide a comparable set of reserve trees (i.e., size and crown distribution) to those left in treated units.

In the lab, increment cores were mounted on grooved boards and hand polished with fine sandpaper. I estimated tree age at breast height by reading annual rings from the cores. Sapwood width, inside-bark bole radius, and annual radial increment of the last 20 years were measured to the nearest 0.01 mm. I made these measurements using a microscope mounted on a dendrochronometer with a Velmex sliding stage and Accurite measuring system. I computed inside-bark basal area (BA), sapwood basal area (SA), and 5-, 10- and 20-year basal area increment (BAInc5, BAInc10 and BAInc 20, respectively) by considering DBH and bark thickness at breast height. BAInc10 represented the gain in growth since treatments were applied. I calculated growth efficiency (GE) as an index of tree vigor. Growth efficiency has been defined as the individual tree's stemwood increment per unit of foliage or leaf area (Waring, 1983). However, SA was used as a surrogate for leaf area, based on the established allometric relationship between these two variables (Seymour and Kenefic, 2002; Woodall et al., 2003). In computing GE, I divided the basal area increment of the last 5 years (BAInc5) by the current sapwood basal area (SA). Furthermore, I classified trees into three age-classes: trees older than 100 years (Presettlement), trees between 50 and 100 years old (Mature), and trees younger than 50 years (Young). The designation of trees older than 100 years as "Presettlement" was intended to reflect the disruption of historic fire disturbance regimes that took place with the onset of significant fire suppression efforts initiated circa 1900 (Arno et al., 1995a).

Each square plot (50x50 to 60x60-m) was further divided into 5x5-m sub-plots to census seedling abundance. To assess post-treatment seedling recruits, I only considered trees less than 10 years old, based on field examination of annual internodes. I also visually estimated the percent cover of shrubs, grasses and woody debris to the nearest 10%. These local stand variables, along with basal area at breast height (BA) and sapwood basal area at breast height (SA) were used in the analysis of spatial correlation described below. I made use of stem maps to compute BA and SA within each 25-m^2 sub-plot.

5.2.3 Data analysis

5.2.3.1 Analysis of treatment effects using classical ANOVA

I compared differences in the response variables (BAInc10, GE and abundance of recruited seedlings) among Harvest-only, Harvest-Burn and Control treatments using a randomized block design with the plot-level means. Distributional assumptions of ANOVA were graphically assessed and heteroscedasticity of variances was tested using Levene's statistic (Sokal and Rohlf, 1995). I found heteroscedasticity in BAInc10 and GE, for which I used square-root transformations. Additionally, I conducted an ANOVA for BAInc for the 10-year period prior to treatment application. I found non-significant a priori differences among the treatments (p=0.434), and therefore assumed pretreatment similarities across experimental units. Mean comparisons among treatments were performed with a Tukey post-hoc procedure (α=0.05). All statistical analyses comparing treatments to Controls (using standard ANOVA) were conducted based on the tagged trees only in Controls.

5.2.3.2 Analysis of age and treatment effects using spatial ANOVA: Statistical background

One difficulty with including age-class as a covariate in my analysis is that the experimental unit is actually not a tree, but a plot. In classical ANOVA this means that we have a sample size of 9 units (3 plots for each treatment) for examining differences between the treatments, even though there are 409 trees on which measurements have been made. If I were to conduct the analysis as if our sample size was the 409 trees, I would be committing what Hurlbert (1984) described as "pseudo-replication", by incorrectly considering the trees as the experimental units when treatments were actually *applied* at the plot level. In this experiment, blocks were first grouped according to similarities among habitat characteristics to primarily account for any spatial structure. Afterwards, the three treatments (Harvest-only, Harvest-Burn, and Control) were randomly assigned to each block. This is a classic randomized block experiment leading to a randomized block design (RBD) with model given by:

$y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$,

where the α_i's (i = 1; 2; 3) represent the 3 treatment effects and the β_j's (j = 1; 2; 3) represent the 3 block effects.

If I still want to consider the individual trees as experimental units, my inferences will be limited to the population of 9 plots used in the experiment. I would then need to treat this study as a case study. Nonetheless, through the use of similar experiments producing consistent results, such findings can contribute to a larger scope of inference regarding the process being studied.

5.2.3.3 Spatial autocorrelation and spatial ANOVA model

With the trees as experimental units, I must further consider that these trees are not likely to be independent in terms of the response variables I might measure on them, such as BAInc and GREFF. In fact, the values of these variables may be the result of a combination of microsite, local competition and other highly spatially autocorrelated factors (Legendre, 1993). Due to these potential spatial correlations, I needed to alter the covariance structure on the residuals of the RBD ANOVA at the tree-level to reflect these inherent spatial correlations. This is done through the use of a spatial ANOVA model.

To characterize the spatial autocorrelation present in the response variables among the trees within a plot, I computed empirical semivariograms (see below). These semivariogram models can then be used to estimate the covariances between the response variable values for any two trees. These covariances are then formed into a matrix of covariances among all the 550 trees (tagged and not tagged in the Control unit). For 550 trees, such a matrix is 550x550, where the $(i, j)^{th}$ entry represents the covariance between the i^{th} and j^{th} tree response values. Denoting this matrix V and treating the ANOVA model as a regression model, we obtained the following linear model with age-class as a covariate for the scenario described:

$$\begin{aligned}
&y_{ijk} = \beta_0 + \beta_1 Z_{1jk} + \beta_2 Z_{2jk} + \beta_3 W_{i1k} + \beta_4 W_{i2k} + \beta_5 A_{1k} + \beta_6 A_{2k} + \beta_7 Z_{1jk} W_{1k} + \beta_8 Z_{1jk} W_{2k} + \\
&\beta_9 Z_{2jk} W_{1k} + \beta_{10} Z_{2jk} W_{2k} + \beta_{11} Z_{1jk} A_{1k} + \beta_{12} Z_{1jk} A_{2k} + \beta_{13} Z_{2jk} A_{1k} + \beta_{14} Z_{2jk} A_{2k} + \varepsilon_{ijk}; \\
&i = 1,2,3;\ j = 1,2,3, \quad \textit{where}:
\end{aligned}$$

y_{ijk} = *the* k^{th} *response for the* i^{th} *treatment in the* j^{th} *block;*

$$Z_{1jk} = \begin{Bmatrix} 1 & \textit{if Harvest - only} \\ 0 & \textit{if Control} \end{Bmatrix}; \qquad Z_{2jk} = \begin{Bmatrix} 1 & \textit{if Harvest - Burn} \\ 0 & \textit{if Control} \end{Bmatrix};$$

$$W_{i1k} = \begin{Bmatrix} 1 & \textit{if block}\,2 \\ 0 & \textit{if block}\,1 \end{Bmatrix}; \qquad W_{i2k} = \begin{Bmatrix} 1 & \textit{if block}\,3 \\ 0 & \textit{if block}\,1 \end{Bmatrix};$$

$$A_{1k} = \begin{Bmatrix} 1 & \textit{if age} = \textit{Mature} \\ 0 & \textit{if age} = \text{Presettlement} \end{Bmatrix}; \qquad A_{2k} = \begin{Bmatrix} 1 & \textit{if age} = \textit{Younger} \\ 0 & \textit{if age} = \text{Presettlement} \end{Bmatrix};$$

β_i = *the* i^{th} *parameter value to be estimated; and*

ε = *the vector of residuals, where* $\varepsilon \sim N(0, V)$.

This generalization of the covariance matrix to include the spatial covariances present affects the parameter estimates, their variances and covariances, and hence all estimated contrasts, ANOVA sums of squares, confidence intervals, and significance tests.

I used semivariogram models to estimate the covariances between the response variable values for any two trees. The estimated semivariogram is defined as:

$$\hat{\gamma}(h) = 1/2 \cdot N(h) \cdot \sum_i [z(x_i) - z(x_i + h)]^2,$$

where h is the lag distance between sampled trees, $N(h)$ is the number of paired comparisons at lag h, and $z(x_i)$ and $z(x_j)$ are the observed tree variable values at location x_i and x_j, respectively (Webster and Oliver, 2001). Under a typical spatial dependence model, two units that are close together will tend to have a smaller variance of the difference. As units get further apart, their differences become larger and usually the variance of the difference becomes larger. In a semivariogram, the semivariance (γ(h)) is plotted on the y-axis against lag distance (h) on the x-axis. The lag distance is the step-size used, and the active lag denotes the largest distance considered between points in the semivariance data set, though the whole data set is included in the analysis (Isaaks and Srivastava, 1989; Rossi et al., 1992). I used a minimum lag distance of 1-m, and active lag of 25-35-m on average (i.e., half of the minimum plot dimension). Empirical semivariograms were computed for BAInc10 and GREFF for each treatment.

I considered single spherical theoretical models for modeling empirical semivariograms, with three parameters known as the nugget, sill, and range. The nugget is a measure of the microscale variation in the response. The sill, or total sample variance, is the ordinate value at which the semivariogram becomes flat. The range represents the distance beyond which samples are spatially independent (Isaaks and Srivastava, 1989; Webster and Oliver, 2001). I used an iterative non-linear weighted least squares procedure with weights proportional to N(h) to fit the variogram model to the empirical semivariograms (Cressie, 1985). Each empirical semivariogram was modeled with biologically meaningful parameters (i.e., non-negative or extremely large parameter values).

Table 5-2 Classical ANOVA results for basal area increment of the last 10 years (BAInc10), growth efficiency (GE), abundance of recruited seedlings per hectare for ponderosa pine (PP) and Douglas-fir (DF), and seedling ratio (PP density/DF density) 10 years after the application of treatments in the Lick Creek Experimental Area, western Montana.

Sources	df	SS	MSS	F-value	Pr (>F)
Sqrt (BAInc10)					
Treatments	2	0.4739	0.2369	10.511	0.0256
Blocks	2	0.0897	0.0448	1.989	0.2514
Residuals	4	0.0902	0.0225		
Sqrt (GE)					
Treatments	2	0.0243	0.0121	8.8566	0.0339
Blocks	2	0.0029	0.0014	1.0498	0.4301
Residuals	4	0.0055	0.0014		
PP seedlings					
Treatments	2	6301.61	3150.82	11.59	0.022
Blocks	2	1513.60	756.81	2.79	0.174
Residuals	4	1087.82	271.90		
DF seedlings					
Treatments	2	4648.75	2324.32	2.18	0.229
Blocks	2	16248.73	8124.36	7.62	0.043
Residuals	4	4266.71	1066.71		
Seedlings ratio					
Treatments	2	21.66	10.83	0.94	0.462
Blocks	2	26.72	13.36	1.16	0.401
Residuals	4	46.09	11.52		

Species codes, ponderosa pine: PP; Douglas-fir: DF.

5.2.3.4 Analysis of new seedling recruitment

Because seedling abundance data often exhibit spatial autocorrelation, statistical assumptions of independence would be violated if we were to consider each of our 5x5-m subplots as being an independent sample (Legendre, 1993). I therefore used a partial Mantel test (Mantel, 1967) to examine the partial correlation of seedling abundance for both species (ponderosa pine and Douglas-fir) with local stand characteristics. The partial Mantel statistic measures the correlation between two variables in space while controlling for the spatial autocorrelation. In this case the test controls for spatial autocorrelation in the two variables of interest (seedling abundance and one of the local stand variables). To conduct this partial Mantel test, the correlation is computed between three *n* by *n* difference matrices, A, B, and C, where one matrix might represent spatial distances between trees, and the other two would represent differences between seedling abundance and BA among subplots, for example. The test statistics are computed by constructing a matrix of residuals, A, for the regression of A on C, and another matrix of residuals, B, for the regression of B on C (i.e., A and B are proper variable difference matrices, while C is a proper distance matrix). The two residual matrices A and B are then compared by a standard Mantel test, where the null hypothesis is that the observed relationship between the two matrices could have been obtained by any random arrangement in space of the observations through the study area (Cressie, 1993; Fortin and Gurevitch, 2001). For each 25-m^2 subplot, I recorded BA (cm^2), SA (cm^2), and percent cover (%) of shrubs, grasses, and woody debris. I considered the (x,y)-coordinates of the subplot center as the spatial location of all the variables. Partial Mantel tests, classical and spatial ANOVA's, and semivariogram modeling were conducted using the statistical software "R" (R-Development, 2004).

5.3 RESULTS

5.3.1 Treatment effects on individual tree growth and vigor

The alternative restoration treatments (Harvest-only and Harvest-Burn) differed in their effect on the growth increment and vigor of residual trees. The harvest-only treatment had the effect of nearly doubling mean basal area increment (BAInc10, 136.58 cm^2) relative to the untreated Control units (75.23 cm^2) ($p<0.05$; Table 5.2 and 5.3; Figure 5.1a). Mean BAInc10 values were also higher following the Harvest-Burn treatment (106.57 cm^2), a 41% increase over tagged trees in the untreated Control. These intermediate values in the Harvest-Burn units were not significantly differerent from either Harvest-only or Control units ($p>0.05$; Table 5.2, 5.3; Figure 5.1a).

Table 5-3 Treatment effects on basal area increment of the last 10 years (BAInc10), growth efficiency (GE), recruited seedling abundance per hectare for ponderosa pine (PP) and Douglas-fir (DF), and seedling ratio (PP/DF) ten years after treatments were applied in the Lick Creek Experimental Area, western Montana. Data are means with SE in parenthesis (n=3). Within a row, means with different letters differ at $P < 0.05$.

	Treatments		
	Harvest-only	Harvest-Burn	Control
BAInc10 (cm^2*tree^{-1}*last 10-years^{-1})	136.576 (19.935) a	106.571 (7.053) ab	75.231 (2.433) b
GE (cm^2*cm^{-2})	.2107 (0.0313) a	0.1453 (0.0069) ab	0.1044 (0.007) b
PP seedlings (#*ha^{-1})	50.93 (17.59) a	67.30 (11.00) a	4.89 (0.89) a
DF seedlings (#*ha^{-1})	73.89 (34.75) a	101.22 (52.21) a	45.56 (35.57) a
Seedlings ratio (PP/DF)	3.80 (3.48) a	0.76 (0.17) a	0.30 (0.13) a

	Blocks		
	1	2	3
BAInc10 (cm^2*tree^{-1}*last 10-years^{-1})	90.458 (5.731) a	108.733 (20.929) a	119.188 (26.667) a
GE (cm^2*cm^{-2})	0.1774 (0.0485) a	0.1407 (0.0252) a	0.1423 (0.0231) a
PP seedlings (#*ha^{-1})	35.56 (17.36) a	58.93 (27.46) a	28.64 (13.08) a
DF seedlings (#*ha^{-1})	132.96 (11.66) a	37.67 (29.50) b	50.03 (21.57) b
Seedlings ratio (PP/DF)	0.25 (0.11) a	4.05 (3.35) a	0.56 (0.20) a

Our measure of tree vigor, mean growth efficiency (GE), displayed similar trends among the alternative treatments. Mean GE of trees in the Harvest-only treatment (0.211 cm^2*cm^{-2}) was significantly greater than Control (0.104 cm^2*cm^{-2}) ($p<0.05$; Table 5.2 and 5.3; Figure 5.1b), whereas GE values in the Harvest-Burn treatment units (0.145 cm^2*cm^{-2}) were intermediate between Harvest-only and Control ($p>0.05$; Table 5.2, 5.3;

Figure 5.1b). Block effects were not significant for either BAInc10 or GE (Table 5.2 and 5.3).

5.3.2 Variation in basal area increment and growth efficiency with tree age (spatial model)

After adjusting group means to account for autocorrelation with the spatial ANOVA model analysis, similar trends were again detected among the treatments means. In this analysis, mean BAInc10 values were again highest in Harvest-only units and intermediate in Harvest-Burn, but differences were significant between all treatments (Table 5.4 and 5.6; Figure 5.2a and b). For the analysis of tree vigor, values for mean GE were intermediate in Harvest-Burn units, and significantly lower than in Harvest-only.

I also detected significant age-class effect ($p<0.0001$; Table 5.4 and 5.5) for both BAInc10 and GE. Growth rates (BAInc10) were highest in the oldest age class, with higher mean values observed for Presettlement trees across all treatments relative to postsettlement trees (Table 5.5; Figure 5.3a). There was not a significant interaction of age-class and treatment for BAInc10 (Table 5.4). All three age classes followed the same trend observed for all trees of greatest growth increment in Harvest-only and intermediate values in Harvest-Burn (Figure 5.3a). Mature trees displayed the greatest difference in BAInc10 among alternative treatments. Mean values for basal area increment in Harvest-only were more than double rates in the Control (Table 5.5, Figure 5.3a). Mean BAInc10 for Harvest-Burn treatment units was over 40% higher than in untreated Control. The Youngest age class showed the least response in BAInc10 to restoration treatments. Means separation tests indicated no significant differences in Young tree BAInc10 among treatments.

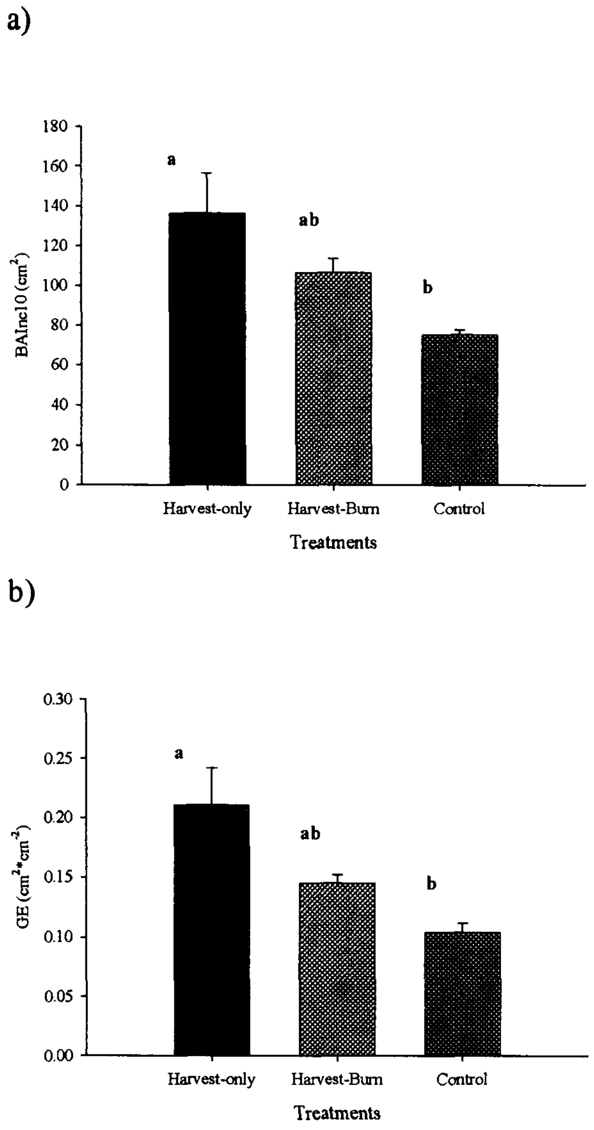


Figure 5-1 Mean treatment effects for (a) basal area increment in the last 10 years (BAInc10), and (b) growth efficiency (GE) of individual trees in the Lick Creek Experimental Area, western Montana. The same letter above the bar indicates no significance differences (i.e., $p>0.05$) among treatments. Error bars represent one standard error ($n=3$).

In the analysis of growth efficiency (GE), significant effects of both age-class and an interaction of age-class and treatment were detected (Table 5.4). Mean GE values as a measure generally decreased with age. GE values were consistently lowest for

Presettlement trees across all treatments. While GE did increase over Controls for both restoration treatments (almost double), these differences were not statistically significant (Table 5.5 and 5.6; Figure 5.3b). For Mature trees, mean GE values were significantly higher in Harvest-only relative to both Harvest-Burn ($p=0.0022$) and Control ($p=0.0001$). Growth efficiency of Young trees was consistently higher than the other age-classes across all treatments ($p<0.0001$; Table 5.5 and 5.6).

Table 5-4 Results of spatial ANOVA for general treatment, block, and age-class effects on basal area increment of the last 10 years (BAInc10) and growth efficiency (GE) for all individual trees in the Lick Creek Experimental Area, western Montana.

BAInc10	d.f.	SS	MSS	F-value	Pr (>F)
Intercept	1	1085.13	1085.13	1156.9506	< 0.0001
Treatments	2	87.59	43.79	46.6924	< 0.0001
Blocks	2	7.08	3.54	3.7740	0.0238
Age-class	2	53.23	26.61	28.3740	< 0.0001
Tmt. X Blocks	4	6.52	1.63	1.7370	0.1410
Tmt. X Age-class	4	5.62	1.41	1.4991	0.2017
Residuals	394	369.54	0.94		
GE					
Intercept	1	533.85	533.85	1219.6007	< 0.0001
Treatments	2	28.79	14.39	32.8832	< 0.0001
Blocks	2	3.23	1.77	4.0353	0.0184
Age-class	2	82.84	41.42	94.6275	< 0.0001
Tmt. X Blocks	4	2.85	0.71	1.6260	0.1669
Tmt. X Age-class	4	5.36	1.34	3.0633	0.0167
Residuals	394	172.46	0.44		

5.3.3 Recruitment patterns

Recruitment of seedlings was generally higher in the Harvest-only and Harvest-Burn treatments than in the Control (Table 5.1). Density of new recruited ponderosa pine (PP) seedlings ranged from 33-87 ha^{-1} in treated units. The mean seedling density of PP varied among treatments ($p<0.05$; Table 5.2, Figure 5.4a). Recruited seedlings were approximately 20% higher in Harvest-Burn when compared with Harvest-only, and more than 10 times higher when compared with Control (Table 5.3). On the contrary, the mean abundance of recruited DF seedlings did not vary significantly among treatments showing high variation within treatments ($p>0.05$; Table 5.2, Figure 5.4b). Block effects were significant for DF seedling abundance only (Table 5.3). I found that the ratio of PP:DF recruited seedlings did not vary substantially among treatments, and it was highly variable in Harvest-only ($p>0.05$, Table 5.2 and 5.3), indicating that this ratio is not a stable measure.

The partial Mantel correlation analysis of our field data did not identify significant relationship of new seedling recruitment with any of the local stand characteristics except one (Table 5.7). I did not detect any significant Mantel correlation between overstory competition variables, BA and SA, with the occurrence of new seedlings ($p>0.05$). Similarly, percent cover of shrubs and grasses, which represented competition from understory, did not correlate with seedling abundance after treatments were applied ($p>0.05$). The only variable that did display positive significant correlation with the abundance of both PP and DF was the percent cover of woody debris. This variable was significant in both Harvest-only and Control treatments ($p<0.05$), but not in the Harvest-Burn treatment.

5.4 DISCUSSION

5.4.1 General growth and tree performance following restoration treatments

At the Lick Creek Experimental Area, ponderosa pine responded positively to restoration treatments in the 10 years after treatments were applied, in terms of greater basal area growth increments and improved vigor (i.e., higher growth efficiency). Studies on second-growth ponderosa pine forests have reported significant and positive responses in growth increments following restoration treatments (Kolb et al., 1998; Nagel and O'Hara, 2001; Skov et al., 2004). Positive response in growth increment for ponderosa pine has been related to reduced competition and increased resource availability (Latham and Tappeiner, 2002; McDowell et al., 2003). In means separation tests among treatments, I generally found that only the Harvest-only restoration treatment had significantly higher mean BAInc10 values than to the Control, BAInc10 values for the Harvest-Burn treatment were at an intermediate level, not significantly higher than Control. Previous growth studies have reported similar conclusions (Fiedler, 2000), implying that prescribed burns may reduce or delay tree growth response, relative to harvest without burning. While surface fire was a frequent natural disturbance in these ponderosa pine forests of the northern Rocky Mountains, historically such burns typically occurred during late summer and early fall (Agee, 1993). Prescribed burns in these forests, however, are most commonly applied during spring months under cooler, more moist conditions weather conditions for various reasons including lower risk of escape and better smoke dispersal (Sala et al., 2005). Negative effects of our Spring burn treatments may perhaps be related to crown scorching of reserve trees or damage to tree roots near the surface (Hart et al., 2005). Wyant et al. (1983) found that scorching of lower crown foliage reduced the transpiration surface area, and consequently photosynthetic capacity. Grier (1989) found that early-season Spring burns, conducted while tree root physiological activity is high, can lead to dramatic reductions in fine root biomass on the order of 60%. Hart et al. (2005) also reported that repeated burning (2-yr intervals) reduced fine root length and biomass, and mycorrhizal root biomass relative to unburned controls in northern Arizona. A reduction in growth rates and increase in mortality relative to unburned trees has also been found in other studies of ponderosa pine (Swezy and Agee, 1991; Landsberg, 1994; Busse et al., 2000). On the contrary, when prescribed burns were conducted in the fall, some studies have reported no delayed growth response (Feeney et al., 1998).

Tree vigor as indexed by growth efficiency (GE) was also highest in the Harvest-only treatments, with intermediate levels observed in the Harvest-Burn treatment. GE is affected by stand structure and light environments within the canopy (Roberts et al., 1993; O'Hara, 1996; Woodall et al., 2003), and trees in Control units presumably experienced higher levels of competition, leading to a reduction in vigor. The fact that we did not find significant differences between the Harvest-Burn and the Control treatments may again be reflecting negative effects of burning. In addition to the potential negative effects of fire on scorched foliage and shallow roots, a decline in nitrogen availability in the mid-term (~10 years) might be another mechanism explaining the difference in GE between Harvest-only and Harvest-Burn (see below). I can hypothesize that the release from competition may have been neutralized by the potential alteration of physiological functions caused by fire (mentioned above), as has been stated in other studies (Sutherland et al., 1991; Swezy and Agee, 1991). Furthermore, the potential alteration of physiological functions may also concern the concentration of mineral soil nitrogen, which can affect photosynthetic capacity levels. Although some studies have shown short-term increases in mineral soil nitrogen concentration after fire (Monleon et al., 1997; DeLuca and Zouhar, 2000; Choromanska and DeLuca, 2001), several indices of nitrogen availability and transformation rates have exhibited a decline in the mid-term (~10 years) after fire (Monleon et al., 1997; Wright and Hart, 1997; DeLuca and Zouhar, 2000; Kaye et al., 2005). Because leaf nitrogen content directly impacts leaf properties and photosynthetic capacity (Reich et al., 1997), direct and indirect effects of different management practices on soil nitrogen availability may have lasting consequences for the physiological performance of ponderosa pine.

5.4.2 Age-class effects on growth increment and growth efficiency

All three age-classes appeared to benefit from restoration treatments relative to the untreated Control for both growth increment (BAInc10) and individual tree vigor (GE). The same trend highest values for Harvest-only, intermediate for Harvest-Burn, and lowest for Control. Such differences were not significant among treatments for BAInc10 of Young trees, nor for GE of Presettlement trees. Contrary to long-held assumptions that tree growth rate is limited by age (Kira and Shidei, 1967; Weiner and Thomas, 2001), and hence old trees may not respond to reductions in competition, I found that Presettlement trees did positively respond to Harvest-only treatments for BAInc10. These findings agree with those of a few other studies dealing with old ponderosa pine trees (Fiedler, 2000; Latham and Tappeiner, 2002; McDowell et al., 2003). McDowell et al. (2003) found that stand density reductions resulted in increased growth of old ponderosa pine trees due to changes in water availability and stomatal conductance. Latham and Tappeiner (2002) reported significant growth responses after thinning for old-growth trees of both ponderosa pine and Douglas-fir in western Oregon. However, in northern Arizona, Skov et al. (2005) found a lack of short term growth response to thinning for their older "presettlement" trees (150-450 years old) three years after treatment. I concur with Latham and Tappeiner (2002) that the idea that old trees do not respond to release treatments is due to the fact that most studies on these trees have been focused on stand volume growth rather than individual tree growth.

However, growth efficiency (GE) of Presettlement trees did not increase in to restoration treatments to the same extent that BAInc10 did. While there was a slight increase in GE observed in restoration treatments relative to Control units, the differences were non-significant. Across all treatments, GE of Presettlement trees was lower than for younger age classes. Lower GE for Presettlement trees might be associated with various proposed causes of growth decline in older trees, including increasing allocation foliar respiration and to belowground storage parts (Ryan et al., 2004). Furthermore, our estimates of growth efficiency based on SA do not account for a potential shift in toward greater ratio of SA per unit foliage area in older trees to compensate for hydraulic limitations imposed by tree height (Ryan et al., 2004). While younger age classes had higher GE values generally, Mature and Young age-class trees appeared to be more negatively affected by burns. Lower crown trees may have been scorched during burns, losing some productive capacity with any reduction in foliage biomass (Wyant et al., 1983). In some cases, managers may wish to conduct prescribed burns in such a way as to control flame lengths to reduce the probability that crowns of Mature and Young trees will be scorched.

Table 5-5 Results of multiple comparisons among treatments for basal area increment of the last 10 years (BAInc10) and growth efficiency (GE) by age-class accounting for spatial autocorrelation, 10 years after treatments were applied in the Lick Creek Experimental Area, western Montana. Age-classes are Young (< 50 years), Mature (between 50 and 100 years), and Presettlement (> 100 years) trees. For multiple comparisons see Table 6. Data are means with SE in parenthesis (*n* varies by treatment and age-class). Within a row, means with different upper-case letters differ at $P < 0.05$ for treatments. Within a column, means with different lower-case letters differ at $P < 0.05/3$ (Bonferoni correction) for age-classes.

BAInc10	n	Harvest-only	n	Harvest-Burn	n	Control	
Young	16	70.281 (11.285) Aa	53	45.204 (16.512) Aa	18	34.305 (14.646) Aa	49.930 (8.263) a
Mature	113	161.682 (7.388) Ab	88	112.152 (6.452) Bb	71	79.288 (6.428) Bb	117.708 (3.909) b
Presettlement	13	174.600 (15.860) Ab	20	142.158 (19.583) ABb	21	94.987 (11.740) Bb	137.248 (9.267) b
Total	142	135.521 (6.665) A	161	99.838 (8.773) B	106	69.526 (6.706) C	
GE							
Young		0.3004 (0.0218) Aa		0.2008 (0.0249) Ba		0.1624 (0.0208) Ba	0.2212 (0.0130) a
Mature		0.2020 (0.0144) Ab		0.1426 (0.0128) Bab		0.1240 (0.0133) Ba	0.1562 (0.0078) b
Presettlement		0.0859 (0.0306) Ac		0.0790 (0.0341) Ab		0.0414 (0.0181) Ab	0.0688 (0.0164) c
Total		0.1961 (0.0135) A		0.1408 (0.0160) B		0.1092 (0.0131) B	

Note: Control includes tagged trees only within uncut Controls.

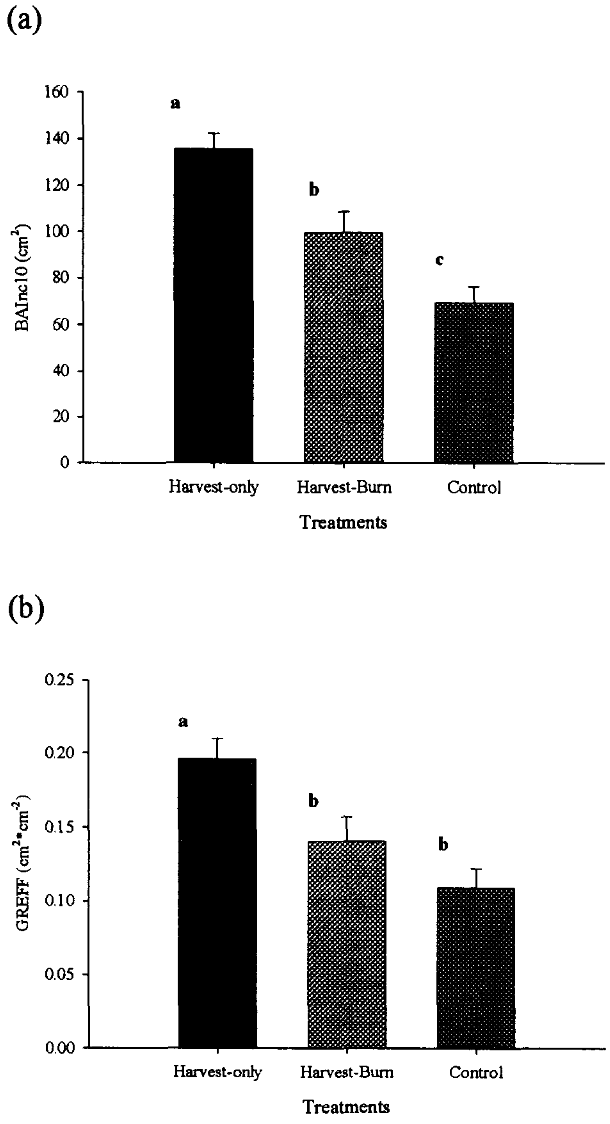


Figure 5-2 Mean treatment effects for (a) basal area increment in the last 10 years (BAInc10), and (b) growth efficiency (GE) of individual trees considering the spatial autocorrelation of all the individual trees for each treatment in the Lick Creek Experimental Area, western Montana. The same letter above the bar indicates no significance differences ($p>0.05/3$) among treatments. Error bars represent one standard error (*n* varies by treatment and age-class).

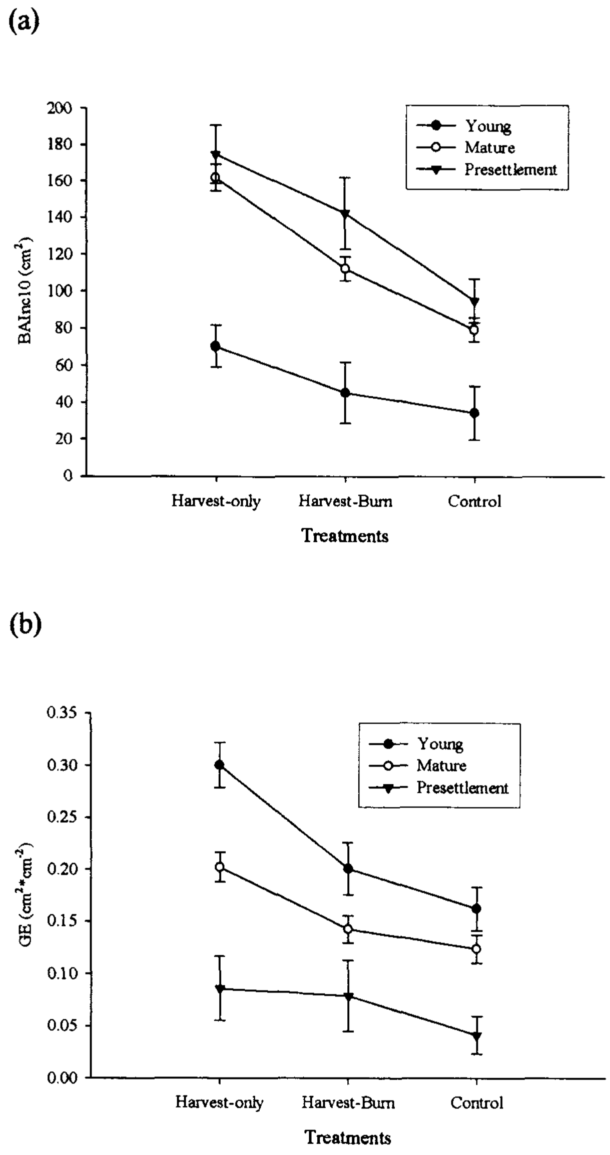


Figure 5-3 Mean treatment effects by age-classes on (a) basal area increment in the last 10 years (BAInc10) and (b) growth efficiency (GE) considering the spatial autocorrelation of all the individual trees for each treatment in the Lick Creek Experimental Area, western Montana. Error bars represent one standard error (*n* varies by treatment and age-class). Age-classes are Young (< 50 years), Mature (between 50 and 100 years), and Presettlement (> 100 years) trees. For multiple comparisons see Table 5.6.

5.4.3 Recruitment of ponderosa pine

Our results suggest that seedlings of ponderosa pine (PP) and Douglas-fir (DF) were adequately recruited during the first ten years after the restoration treatments were applied. Recruitment of PP seedlings increased following restoration treatments relative to Control, with highest levels of both PP and DF recruitment occurring in the Harvest-Burn treatment. These results supported the importance of both a reduction in overstory and understory competition and the reintroduction of surface fires have for conifer regeneration. I did not find any abundance difference between species 10 years after treatment application. The fact that PP seedling recruitment was not more abundant than DF may be explained in that a shift of recruitment dominance can be expected only after periodic fires reduce DF survival rates. I could also speculate that the ponderosa pine system may be resilient to traditional restoration practices. Suding et al. (2004) stated that strong feedbacks between the biotic and the physical environment can alter the efficacy of successional-based restoration efforts. To evaluate whether or not this explanation applies to the current study, further research is necessary. It is plausible to expect that PP regeneration follows masting periods of seed production and dispersal, and therefore the time framework of our study may be too short to capture the processes involved. In northern Arizona, PP recruitment has been associated with climatic conditions. There, regeneration success is promoted by warm and moist conditions in the several years prior to a good seed year, as well as in the first year after. However, these conditions have occurred rarely in the last century (Savage et al., 1996). Tree regeneration rates also depend on cone/seed production periodicity, predation, seed viability, seedbed conditions, and germinant survival among others. In northern Arizona, Bailey and Covington (2002) documented that a sufficient supply of seeds is available for new ponderosa pine regeneration only once or twice per decade.

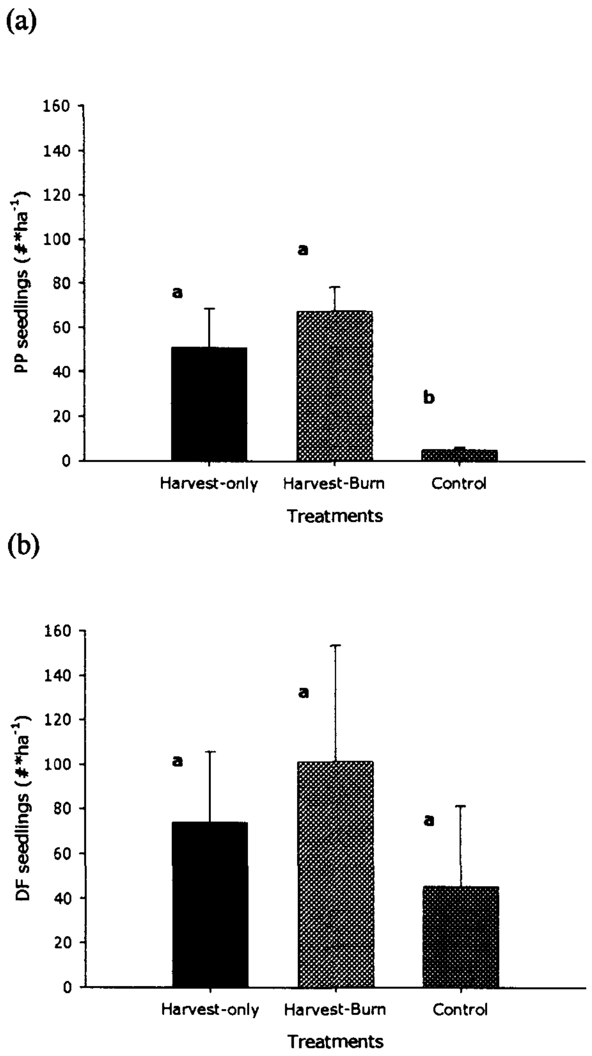


Figure 5-4 Treatment effects on the mean abundance of seedlings (per hectare) recruited post-treatment (<10 years old) for (a) ponderosa pine (PP) and (b) Douglas-fir (DF) in the Lick Creek Experimental Area, western Montana. The same letter above the bar indicates no significant differences (i.e., $p>0.05$) among treatments. Error bars represent one standard error ($n=3$).

Table 5-6 Partial Mantel coefficients P-values for the multiple comparison contrasts based on the spatial ANOVA

Contrast	BAInc10	GE
Harvest-only vs. Harvest-Burn	< 0.0001	< 0.0001
Harvest-only vs. Control	< 0.0001	< 0.0001
Harvest-Burn vs. Control	0.0001	0.1874
Young vs. Mature	< 0.0001	< 0.0001
Young vs. Presettlement	< 0.0001	< 0.0001
Mature vs. Presettlement	0.0671	< 0.0001
Harvest-only vs. Harvest-Burn for Young	0.2107	0.0028
Harvest-only vs. Control for Young	0.0524	< 0.0001
Harvest-Burn vs. Control for Young	0.7220	0.7617
Harvest-only vs. Harvest-Burn for Mature	< 0.0001	0.0022
Harvest-only vs. Control for Mature	< 0.0001	0.0001
Harvest-Burn vs. Control for Mature	0.0494	0.8208
Harvest-only vs. Harvest-Burn for Presettlement	0.1987	0.8809
Harvest-only vs. Control for Presettlement	0.0001	0.2116
Harvest-Burn vs. Control for Presettlement	0.0665	0.7901
Young vs. Mature under Harvest-only	< 0.0001	0.0001
Young vs. Presettlement under Harvest-only	< 0.0001	< 0.0001
Mature vs. Presettlement under Harvest-only	0.4630	0.0005
Young vs. Mature under Harvest-Burn	0.0002	0.0186
Young vs. Presettlement under Harvest-Burn	0.0002	0.0036
Mature vs. Presettlement under Harvest-Burn	0.1461	0.0675
Young vs. Mature under Control	0.0052	0.0565
Young vs. Presettlement under Control	0.0011	< 0.0001
Mature vs. Presettlement under Control	0.2452	< 0.0001

I found greater post-treatment seedling abundance than reported by Bailey and Covington (2002) for northern Arizona, although the time-frame is different. They found only 18-41 seedlings*ha^{-1} in treated areas (thinning) in the absence of fire, and only 12 seedlings*ha^{-1} 1-yr after burn treatments were applied. In my study, the recruitment of both species appeared to benefit from Harvest-Burn (in absolute terms), and was locally associated with the percent cover of woody debris in Harvest-only and Control treatments. Successful tree establishment has been reported to depend on the creation of a "safe site" such as the ash bed of a consumed log, where seedlings could establish and grow (Dieterich, 1980; Smith et al., 1997). Additionally, in the absence of fire, the presence of woody debris can also benefit the establishment of PP and DF. Woody debris may reduce high temperatures near the soil and increase humidity levels. However, further work is needed to understand the causal relationship between woody debris and establishment and growth of seedlings. In this study of regeneration ten years after restoration treatments I was unable to discern effects of local competition effects on seedling abundance at the scale examined; no correlation was found between seedlings abundance and local stand characteristics for either species. Fajardo et al. (*in press*) found that the spatial association between saplings of PP and DF and the overstory trees depended on the size of overstory trees and the moisture-level of the site under study.

5.4.4 General implications

Few studies in the northern Rockies have examined ponderosa pine response to forest restoration. My results indicate that the growth and performance of ponderosa pine respond positively to these restoration practices, particularly for harvest without burns. I can suggest that burning, which negatively affected mainly Mature and Young trees, should be applied carefully in restoration treatments so that surface fires do not reach the crowns. However, harvest with burning appeared to favor new recruitment, particularly ponderosa pine. I can expect a trade-off of management goals when dealing with burns; if growth and performance of residual trees are our objectives, burning may be a detrimental practice; if recruitment is our main goal, burning may become beneficial.

Table 5-7 Partial Mantel coefficients of correlation and probability values for abundance of recruited seedlings (<10-years old) and local site variables (basal area (BA), m^2*m^{-2}; sapwood (SA), cm^2*m^{-2}, and percent cover of shrubs, grasses and woody debris cover) in the Lick Creek Experimental Area, western Montana. BA and SA were scaled up to m^2 relative to the size of the 25-m^2 subplots.

		Ponderosa pine seedlings		Douglas-fir seedlings	
Treatment	Variable	r	Pr (> F)	R	Pr (> F)
Harvest	BA	-0.0134	0.2557	-0.0125	0.2677
	SA	-0.0086	0.3357	-0.0072	0.3676
	Shrub	0.0085	0.2867	0.0085	0.2797
	Grass	0.0088	0.2807	0.0089	0.2527
	Woody Debris	0.0298	0.049	0.0314	0.0439
Burn	BA	-0.0111	0.3087	-0.0106	0.2657
	SA	-0.0062	0.3906	-0.0051	0.4056
	Shrub	0.0122	0.1728	0.0121	0.1988
	Grass	0.0064	0.3197	0.0069	0.3037
	Woody Debris	0.0204	0.1049	0.0219	0.1189
Control	BA	-0.0102	0.3277	-0.0092	0.3447
	SA	-0.0037	0.4136	-0.0022	0.4915
	Shrub	0.0040	0.3946	0.0041	0.3716
	Grass	0.0103	0.2587	0.0100	0.2617
	Woody Debris	0.0331	0.0467	0.0343	0.0370

Chapter 6

GENERAL CONCLUSIONS

6.1 OBJECTIVES ACCOMPLISHED

In Chapter 2 "Effects of natural and human disturbances on the dynamics and spatial structure of *Nothofagus glauca* (Phil.) Krasser in south-central Chile", I used spatial statistical analysis through the Ripley's *L*-function, from which I obtained a sound structural description for the different stands under study. This structural description along with some complementary analyses (e.g., dendrochronology and diversity indices) helped me to characterize the dynamics of each individual stand, and to compare them among sites of different disturbance-origin and by that to test the *Nothofagus* regeneration model (objective Ch. 2a). *Nothofagus glauca* occurred in both sites experiencing coarse-scale disturbance and harsh site conditions (objective Ch. 2b). In particular, I found that the composition, structure and spatial association of *N. glauca* relative to companion species can all vary as a function of the disturbance origin of the site (objectives Ch. 2c and 2d). I concluded the chapter stating that the description of spatial association among different species should be considered a required first step to account for species coexistence under different stand structures. The clear positive association between seedlings and overstory trees at the landslide site (the harshest site) in contrast to the other sites where such a trend was not observed, along with the pioneer nature of this species (objective Ch. 2e), exemplified the additive role spatial analysis has in descriptive studies.

In Chapter 3, "Ponderosa pine and Douglas-fir regeneration spatially associated with moisture-level in managed uneven-aged forests of western Montana, U.S.A.", I found that saplings are distributed in clumps across all sites (objective Ch. 3a), that ponderosa pine and Douglas-fir are not spatially disassociated with one another (objective Ch. 3b), and that the spatial association between saplings and older cohorts is relative to the size-class of overstory trees (objective Ch. 3c). I used an index of association based on the bivariate version of Ripley's *L*-function. By using this index of association (IA), I was able to numerically distinguish different spatial associations between saplings and overstory trees (objective Ch. 3d). By including this novel methodological strategy (i.e., the index of association), I made an extension in the scope of the same spatial analysis used in Chapter 2. Beyond a qualitative observation of the spatial pattern, but I assigned a quantitative value to the degree of association. This examination allowed me to compare various sample plots in separate groups, and thereby find particular support for a specific competition/facilitation model under differing levels of moisture availability.

In Chapter 4 "Distinguishing microsite and competition processes in even-aged tree populations by using spatial autocorrelation analysis", I separated two tree-tree interaction processes (i.e., microsite versus competition effects) that were previously not clearly distinguished for tree populations (objective Ch. 4b). The assignment of a dominant driving process of plant interaction at a given time led me to hypothesize a population development model based on the predominance of competition and/or facilitation effects on neighbor trees through time. The stand development model worked well for young ponderosa pine plantations (objective Ch. 4a). Furthermore, given logically derived *a priori* hypotheses, I showed that it is possible to accurately determine causal factors for field measured data. I used geostatistics (i.e., semivariograms) to depict and discriminate the spatial autocorrelation of a tree variable, an approach used only once before (Bachacou and Decourt, 1976). This semivariogram modeling approach resembles the index of association (IA) introduced in Chapter 3, for it allows us first of all to numerically account for the spatial observed pattern, and secondly to make analytical comparisons among different cases. This improvement in the strategic use of spatial statistical tools offers better insights in how we can depict and interpret ecological patterns (objective Ch. 4c).

Finally, in Chapter 5 "Growth, performance and recruitment response of ponderosa pine to restoration practices in Lick Creek Experimental Area", I dealt in particular with two key topics, 1) effectiveness of ecological restoration treatments, and b) the response of old trees to release from competition. Utilizing a field experiment established to evaluate alternative restoration practices of comprehensive thinning with and without subsequent broadcast burning (objective Ch. 5a), I developed a spatial analysis methodology (Spatial ANOVA) that included all the observations (trees) located in each experimental unit as a covariate. For this it was necessary to recognize and incorporate into the spatial ANOVA model the intrinsic spatial autocorrelation (i.e., dependency of observations) of the tree variable under study. Additionally, by using this more correct approach, I was able to add the tree age-class as a separate factor to the spatial ANOVA model (objective Ch. 5b). Particularly, this approach allowed me to interpret the effect of restoration treatments on old trees, and to account for both their positive response to the release from competition and potentially negative effects of spring burning (objective Ch. 5c). Ponderosa pine seedling recruitment was also affected by restoration treatments (objective Ch. 5d), and positively correlated with the percent cover of woody debris (objective Ch. 5e).

6.2 GENERAL DISCUSSION

The complexity of the forest system, involving intra- and/or interspecific plant interactions along with the influence of abiotic factors, creates a mosaic of patterns that is not always explicitly interpretable. I have taken this complexity as a challenge and sought to disentangle the many questions forest ecosystems present to us, and attempted to determine and interpret the causal factors explaining observed patterns. For this reason, I have worked through the chapters of this thesis on empirical evidence to develop the general objective of linking spatial observed patterns and underlying forest ecological processes by using spatial statistical tools. The relationship between observed spatial pattern and responsible process is not always easiliy established. The lack of a clear link between pattern and process can be succinctly explained in three ways: 1) various processes may create the same pattern (Cale et al., 1989; Wyszomirski et al., 1999); 2) causality may not be fully straightforward (Rees et al., 1996; Turner et al., 2001); and 3) processes may also be the result of specific patterns (Turner, 1989). In the different chapters of this thesis I have dealt with this research issue by both elaborating spatial analysis strategies to cope with autocorrelated data, and by testing logically derived hypotheses about ecological patterns. The findings from this work, which have resulted from the application of spatial pattern analyses in various forest ecosystems, hold promise on the general scope and effectiveness, and particularly on the flexibility these methodologies have to cope with field data. With these results I have demonstrated that particular research questions can be solved solely by using spatial pattern analyses, and not only in a complementary fashion.

6.2.1 New contributions

The use of spatial patterns to assess underlying process is not new in forest ecology; it is actually the very seminal approach of early ecologists to understand plant systems (Gleason, 1926), i.e., to describe a pattern and generate hypotheses on the causation of it (Turner, 1989). However, the novelty of my study has to deal with the new strategies adopted to make sounder inferences on the links between pattern and process. These new strategies included the index of association, the semivariogram approach, and the spatial ANOVA model in forest field experiments. These strategies represent real and new contributions to forest ecology and management.

In Chapter 2, the study of spatial associations between the dominant tree species *Nothofagus glauca* and its companion species can give a preliminary understanding on ecological requirements of this particular species and on interactions with other species. *Nothofagus glauca* belongs to a climatic and ecological transitional area, highly populated, in central-south Chile and it has been poorly studied so far (Donoso, 1996; Veblen et al., 1996b). These characteristics make any attempt to describe its ontogeny and its relation with disturbances a helpful background to create and develop ways to manage and protect this forest type resource.

In Chapter 3, the spatial association found between saplings and overstory, which depended on the moisture-level of each site, can lead to important consequences on the expectations we can hold regarding selection harvests. For example, the creation of gaps for stimulating seedling arrivals in dry sites can be seen as an erroneous target practice for these ponderosa pine and Douglas-fir forests. Furthermore, selection harvests appeared to favor the recruitment of both ponderosa pine and Douglas-fir.

In Chapter 4, the use of semivariogram models to separate the two distinct processes of competition and microsite effects during the early development of tree populations could contribute to understanding the role and timing that each process has on the dynamics of such populations. The importance of microsite in shaping growth and interactions among trees has been largely overlooked. The assumption of resource availability homogeneously distributed in the field can be viewed as a naïve perspective that obscures the actual picture of tree-tree interactions. Even though the recognition of microsite importance can have consequences on the timing of thinning, I anticipate logistical and economic constraints to practicing thinning on local-scales based on microsite differences. Thinning is an activity also based on a cost-benefit economical relationship, and consequently is typically practiced at stand level or larger scales.

In Chapter 5, the evaluation of restoration efforts by measuring growth and vigor of residual trees and seedling recruitment can have enormous implications into future management planning. First, evaluations of restoration efforts are still scarce, particularly for forest communities. Second, the results obtained are not only helpful for restoration purposes but for general silvicultural practices for this uneven-aged forest type. Third, ecologically speaking, the evaluation of restoration practices constitute a test for major ecological theories, particularly for those based on successional-driven communities (Bradshaw, 1987; Suding et al., 2004). Regarding old trees, by using a novel analysis approach (i.e., spatial ANOVA) for forest field experiments, I was able to corroborate that old trees do respond to release of competition. This finding, along with the ones from other studies, highlights the importance of old trees to structure and dynamics in forest stands, particularly in terms of carbon sequestration (Carey et al., 2001).

6.2.2 Future studies

Finally, the lines of investigation that this study can promote are diverse. One of them might be related to the formal incorporation of spatial patterns and spatial autocorrelation into forest stand modeling. Many forest stand models are distance-dependent-based, which means they have some measure for tree competition incorporated, e.g., an index of competition or and index of clustering. However, both indices are not particularly dynamics in time, and may also carry some spurious correlation due to the lack of observation dependency (e.g., competition indices). Another line of research would deal with the development of spatial relationships between patterns and processes by using additional techniques that can result in sounder causal inference, e.g., path analysis and structural equations. In this respect the development of logically derived *a priori* hypotheses based on well-planned observational studies is necessary. One additional line of research that could be followed relates to an inter-scale approach. The interpretation of patterns relies on the scale the study is conducted (Greig-Smith, 1979; Legendre and Legendre, 1998; Dale, 1999). It is also expected that the relationship between pattern and process changes through different scales. For example, in the field of landscape ecology it is expected that patterns can also influence process (Turner, 1989). It is also important to consider microscale patterns at individual tree level. These patterns can potentially be related to ecophysiological processes. The importance of heterogeneity in spatial pattern heterogeneity across different scales should be emphasized in terms of biodiversity and environmental factors.

Chapter 7

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